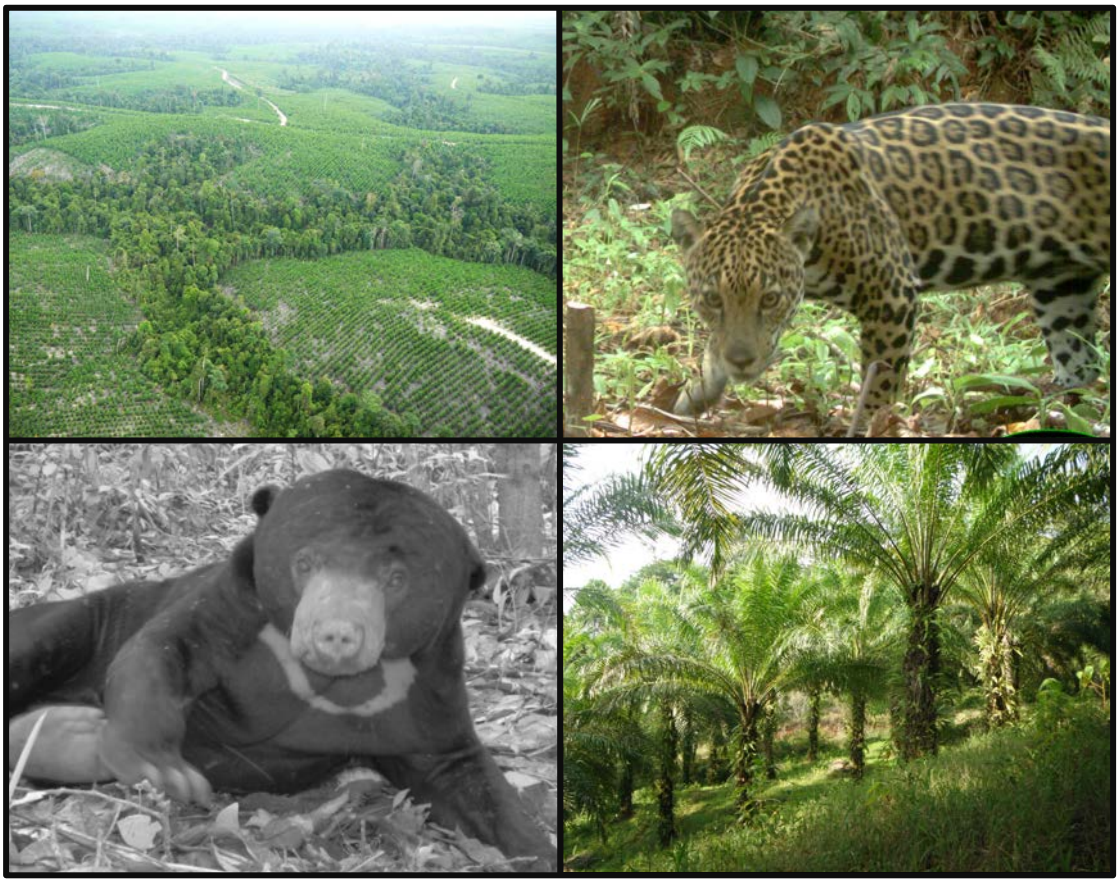
Maintaining connectivity for tropical rainforest mammals in agricultural landscapes



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The field work in Costa Rica involved extremely long, hard days of traversing extensive areas of challenging terrain – hiking in downpours and on very steep (Don't let go!) slopes, stopping every few minutes to empty our water-filled gum boots, hour plus-long drives to get to starting points and back home again each night, riding in boats and canoes, occasionally horses, traversing crocodile infested swamps and rivers, slugging through deep Raphia swamps that would suddenly sink us up to our waists in

water, and pulling kids out of deep mangrove mud that had swallowed their boots. All such events were part of a regular day of field work. Haley Watson, Eduardo Nieto, Luis Gomez and Clara Vignolo all played key roles in this and as much fun as the experience and stories were, I fully appreciate the amount of energy and physical and emotional stamina it required. Haley was with me from beginning to end, including the juggle of research and teaching and minding my ten and twelve-year old boys on days when she was not in the field collecting data. Her focus and creative energy – including down time entertainment of twirling fire donning poi balls, slack lining and banjo playing - made the experience all the better. I can't thank her enough for her resilience and hard work. Eduardo Nieto showed equal commitment to the project, working with us throughout – never tiring, keeping us on track while rotating cameras and coming to know the study area and its residents (the ones he wasn't already related to) in a way that facilitated the many complicated aspects of accessing sites. His ability to have Luis roaring in fits of laughter each night on the drives home is unforgettable. Luis was also fundamental to data collection – helping us with many days of setting and collecting cameras. His cheerful demeanor and skillfulness in remote settings were a fantastic asset to the project. Clara was central to getting the project rolling. She jumped right in at the beginning of the project, expediently speaking to land owners to gain their permission to set cameras on their land. I'm very thankful for her time, energy and language skills in getting the project off the ground.

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Statement of the Contribution of Others

Nature of Assistance	Contribution	Names, Titles and affiliations of co-contributors
Intellectual support	Collaboration	My primary supervisor, Professor William F. Laurance, and secondary supervisor, Dr Gary Paoli, actively collaborated with me throughout the duration of the PhD. Dr Susan Laurance and Dr Jeff Sayer, also secondary supervisors, played a supporting role providing guidance and conversations on my research topics, especially in early stages of the PhD. Other collaborators are mentioned at the start of the individual chapters where appropriate.
	Statistical support	Dr Ainhoa Magrach provided statistical guidance for species richness and community composition analyses for the Sumatra study. Dr Reuben Clements and Dr Chis McClure provided statistical guidance on occupancy modelling analyses for the Sumatra study. Dr Mathias Tobler provided conducted the statistical analyses for the multi-species occupancy and corridor models for the Costa Rica study.
	GIS	Dr Eben Broadbent and Dr Angelica Maria Almeyda Zambrano from the Spatial Ecology and Conservation Lab, University of Florida and provided remote sensed data based on their INOGO Mapas work on the Osa Peninsula and repeat rounds of raster layers representing environmental variables in the study area. Max Villalobos of Osa Conservation provided initial base layers for the Costa Rica study area and early guidance. Craig Furmage assisted in map making for the Sumatra study. Christiane Roetgers assisted in organizing my GIS database during fieldwork in Costa Rica.
	Editorial assistance	Professor William F. Laurance and Dr Gary Paoli provided editorial assistance throughout the thesis and duration of the PhD. Professor Susan Laurance provided editorial assistance for Chapter 2. Dr Mason Campbell provided editorial assistance for Chapters 5, 7 and 8 and a general overview of the entire thesis. Co-authors of published papers (as noted at the beginning of each chapter) provided editorial feedback on drafts of associated manuscripts.
	Photography	All photos within the thesis were taken by Betsy Yaap and the camera traps placed by the Betsy Yaap and research assistants during the study, except for the top left cover page photo and photos in Figure 4.2, which were taken by Professor William F. Laurance.

Nature of Assistance	Contribution	Names, Titles and affiliations of co-contributors
Financial support	Field research	The Australian Research Council funded the research conducted during this PhD via an Australian Laureate Fellowship awarded to Professor William F. Laurance. Funding was also received from the Mohamed bin Zayed Species Conservation Fund.
	Stipend	I (Betsy Yaap) received an Australian Postgraduate Award to undertake this research.
Data collection	Research assistance	The following people kindly assisted me (for differing durations) with field data collection during my PhD candidacy: In Costa Rica: Haley Watson, Eduardo Nieto, Luis Fernando Quintero Gomez, Clara Vignolo, Andrea Johnson and Esteban Brenes In Indonesia, APRIL employees: Brad Sanders, Muhammad Iqbal, Suwanto, Asben and Zulkifli
	Research sites	In Costa Rica, numerous private landholders and Costa Rica's Área de Conservación Osa (ACOSA) - Sistema Nacional de Areas de Conservacion (SINAC) provided permission to use various field sites, including National Parks, for this research. In Indonesia, the Indonesian Institute of Sciences (LIPI) and State Ministry for Research and Technology (RISTEK) provided permission to conduct this research. Asia Pacific Resources International Limited (APRIL) provided access to their plantations.

Abstract

Across the tropics, agricultural activities and tree plantations are rapidly expanding to meet growing human needs for food, wood and fiber. Such developments are reducing the extent of forests and severing remaining forest blocks, thereby reducing and fragmenting wildlife habitat. Large mammals are particularly vulnerable to such habitat loss and fragmentation because of their large area needs and high susceptibility to poaching and other human pressures. My research focuses on maintaining connectivity for large mammals in fragmented landscapes within two of the world's recognized biodiversity hotspots, the rainforests of central Sumatra, Indonesia and the Osa Peninsula of Costa Rica.

I used camera traps and rapid-survey techniques to investigate the local distribution of larger (>1 kg) mammals, aiming to improve survey methods and devise wildlife-management recommendations in agricultural landscapes. My general objectives were to:

1. Survey the extent and type of scientific research that has been conducted to date on "biological corridors" (remnant or linear vegetation that could provide avenues for wildlife movements or habitat for animal occupancy) in tropical forests; and identify findings of particular relevance for the use of such corridors by larger mammals in the tropics.
2. Assess the efficacy of various rapid-assessment methods used to survey mammals in agricultural and timber-plantation landscapes, by comparing (a) automatic camera traps with without baiting and with (b) data collected from community interviews and from expert opinion.
3. Test the influence of landscape and site variables that could affect the use of biological corridors by individual mammal species, using camera trap data and occupancy models. The influence of factors such as corridor width, length, habitat type, surrounding matrix, and distance to core habitat was tested individually in two broad types of potential biological corridors: (a) linear riparian-forest remnants within an industrial wood-pulp (*Acacia mangium*) planation in Sumatra,

and (b) a mixed-use landscape with a mosaic of natural and agricultural lands between three protected areas on the Osa Peninsula.

My literature review indicates that landscape-scale corridors are a popular conservation strategy in tropical countries, but much of scientific literature on the effectiveness of tropical forest corridors has focused on relatively small spatial scales. The limited scale of these studies precludes an effective analysis of broader ecological processes across more extensive forest landscapes (on the order of >1,000 km^2 or more).

Studies of large mammals in tropical nations largely support the recommendations for corridor design from the more extensive body of literature on temperate-zone corridors. In broad terms, these studies suggest corridor use by large mammals may be enhanced by maximizing corridor connectivity, and minimizing human disturbances that degrade forest quality. Species tend to respond to corridors in species-specific manners, such that individual habitat predictors may influence some species positively while having little or even negative effects on other species. Anthropogenic disturbances such as hunting, logging, transport corridors, settlements, and mining near to corridors generally have a negative impact on corridor use by many species of high conservation significance. The proximity of large forest tracts nearby also has a positive and often strong effect on corridor usage. However, the literature I examined only rarely provided explicit tests of the importance of corridor width and length on corridor efficacy for wildlife occupancy or movements.

I compared the efficacy of three rapid assessment techniques – scent-baited camera traps, community interviews and expert interviews - for conducting rapid assessments of High Conservation Value (HCV) mammals. In particular, I contrasted the value of these rapid-survey approaches for producing an accurate regional-species inventory and effectively identifying the distribution of individual species across landscapes. I found that each method has certain advantages and appears to have varying efficacy for different species and geographic regions; no single method emerged as being consistently superior over the others. Rather, the three approaches appear to provide complementary information in different contexts, and all three have the potential to contribute to rapid HCV mammal assessments.

In Sumatra, I evaluated linear remnants of riparian forest in an industrial *Acacia* plantation, spanning a landscape of about 180 km^2 in area. I evaluated five corridor-design variables for large (>1 kg) mammals: corridor width, corridor length, distance of the sampling point from core forest habitat, direct connectivity with forest core habitat, and habitat type. The results suggest that linear riparian remnants of 100-200 m width can function as habitat and potential movement corridors for many large mammal species in Sumatra, at least for localized movements extending up to a few kilometers from intact forest. This study was the first to assess the habitat and landscape factors that influence the use of linear remnants by the Malay tapir (*Tapirus indicus*).

On a larger scale, in a 740 km^2 area of the Osa Biological Corridor in Costa Rica, I evaluated corridor design-variables for 16 large mammal species, focusing on species' habitat use and distance to nearby core habitats. I identified species-specific responses to six habitat types, demonstrating that the presence of forest had a strong positive effect on occupancy for almost all species. However, the linear distance to large blocks of forest (≥500 ha) was a significant predictor for only a few species, emphasizing the conservation value of retaining smaller, fragmented forests across the corridor. The percentage land-cover of mangroves, grasslands and oil palm surrounding sample sites all had significant negative associations for many species across the large-mammal community. Using least-cost modeling to compare single-species and multi-species corridor models, I found that most corridors developed for single-species showed a strong overlap with the multi-species corridor created based on the average habitat preference of all species. Likewise, there was a minimal change in corridor cost for most species when comparing the multi-species corridor with those designed for single species. The findings from circuit-flow analyses, where I compared models of species movement routes using the same single and multi-species data used in the least-cost models, also supported this conclusion. Therefore, a single corridor designed for multiple species would potentially serve the majority of mammal species on the Osa Peninsula. The integrated approach of intensive landscape-scale sampling with camera traps, multi-species occupancy modeling and corridor modelling in this study is a cost-efficient approach and especially useful for defining regional corridors between

protected areas at a scale ranging from a few hundred to a thousand square kilometres.

This study was the first to sample large mammal use of swamps dominated by the tree *Raphia taedigera*, which is a distinctive habitat type in Central America. My findings revealed that they provide potentially important habitat for maintaining wildlife connectivity across the Osa Biological Corridor.

Collectively, my findings further our understanding of biological corridor-design variables for large tropical mammals in Sumatra and Costa Rica. Rapid survey techniques show considerable promise for evaluating HCV habitats and for documenting species distributions, although each strategy I evaluated has some apparent advantages relative to the others. As detailed above, my results and habitat-management recommendations have a number of practical implications for enhancing large-mammal use in heterogeneous tropical landscapes. Human-dominated landscapes will continue to expand in the tropics, underscoring the importance of devising and implementing landscape-design principles that maximize the use of such lands by larger mammal species and other rare wildlife.

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Chapter 1 Introduction

Background

Across the tropics, agricultural activities and tree plantations are rapidly expanding to meet growing human needs for food, wood and fiber (Hansen et al. 2013, Riitters et al. 2016, Haddad et al. 2015, Abood et al. 2015). Such developments are reducing the extent of forests and severing remaining forest blocks, thereby reducing and fragmenting wildlife habitat (Fischer and Lindenmayer 2007, Laurance et al. 2011, Laurance et al. 2002). Large mammals are particularly vulnerable to such habitat loss and fragmentation because of their large area needs and high susceptibility to poaching and other human pressures (Cardillo et al. 2005, Laurance 1991). My research focuses on maintaining connectivity for large mammals in fragmented landscapes within two of the world's recognized biodiversity hotspots, the rainforests of central Sumatra, Indonesia and the Osa Peninsula of Costa Rica.

I have worked professionally in environment and sustainability consulting since 2008, conducting High Conservation Value (HCV) assessments and mammal surveys in oil palm and *Acacia* plantations for companies seeking third-party sustainability certification and mentoring and peer reviewing other groups' work on the topic. HCVs are defined as biological, ecological, social or cultural values of outstanding significance, or critical importance, at a national, regional or global scale (Brown et al. 2013). The HCV approach is used by third-party certification schemes, such as the Roundtable on Sustainable Palm Oil (RSPO) and Forest Stewardship Council (FSC), private sector organizations, and financial institutions as part of their principles and criteria or investment policies which require identification and protection of HCVs. This thesis is an extension of this work, investigating large-mammal rapid survey techniques and corridor-design variables to improve management recommendations for larger mammals (> 1 kg) in agricultural landscapes. I sought to critically evaluate whether maintaining riparian buffers in plantations and a mosaic of natural and agricultural lands located between larger blocks of forest enabled movement of large mammals across tropical landscapes.

Objectives

I used camera traps and rapid-survey techniques to investigate the local distribution of larger (>1 kg) mammals, aiming to improve survey methods and devise wildlife-management recommendations in agricultural landscapes. My general objectives were to:

1. Survey the extent and type of scientific research that has been conducted to date on biological corridors in tropical forests; and identify findings of particular relevance for the use of such corridors by larger mammals in the tropics (Chapter 2).
2. Identify the efficacy of various rapid-assessment methods used to survey mammals in agricultural and timber-plantation landscapes, by comparing automatic camera traps (a) with and without baiting (Chapter 3) and (b) with data collected from community interviews and from expert opinion (Chapter 7).
3. Test the influence of landscape and site variables that could affect the use of biological corridors by individual mammal species, using camera trap data and occupancy models. The influence of factors such as corridor width, length, habitat type, surrounding matrix, and distance to core habitat was tested individually in two broad types of biological corridors: (a) linear riparian-forest remnants within an industrial wood-pulp (*Acacia mangium*) planation in Sumatra, Indonesia (Chapter 4), and (b) a mixed-use landscape with a mosaic of natural and agricultural lands between three protected areas on the Osa Peninsula, Costa Rica (Chapters 5 and 6).

Focal Crops

This research focused on two tropical tree crops, *Acacia* (*Acacia mangium*) and oil palm (*Elaeis guineensis*), mainly because of their rapid expansion in important, high biodiversity areas (Gaveau et al. 2016, Fitzherbert et al. 2008, Obidzinski and Dermawan 2012, FAO 2014, Carlson et al. 2012). These commodities are also very prominent in the third-party certification market (Nasi and Frost 2009, FSC 2014, RSPO

2016, Yaap et al. 2010) which are voluntary standards that are designed to verify that producers and/or their supply chains are environmentally sustainable.

Tree plantations are common in the tropics, with extensive plantations of rubber, teak and quick growing species for wood-fibre production, such as *Acacia*, found across the tropics. In Indonesia, pulpwood plantations cover millions of hectares of land - estimated at 4.9 million ha in 2010. The country has national targets to triple planted areas to 14.7 million ha by 2030 (Obidzinski and Dermawan 2012, Abood et al. 2015). Large mammal use of linear remnant forests in an *Acacia* plantation in Sumatra's Riau Province was studied to assess the value of 100 - 200 m wide riparian forest remnants for landscape connectivity (Chapter 4). In addition, the efficacy of a commercial scent lure was trialled for surveying mammals in this landscape (Chapter 3).

Oil palm production is also a major driver of deforestation in the tropics, with growing international concern over the environmental and social impact of this highly productive and profitable crop (Fitzherbert et al. 2008, Sayer et al. 2012, Koh and Wilcove 2008, Laurance et al. 2010, Phalan et al. 2009). Indonesia, a global biodiversity 'hotspot' (Myers et al. 2000), is the world's leading producer of palm oil, with 7.4 million hectares harvested in 2014 (FAO 2014). Other tropical countries in Africa and Central and South America are increasingly being targeted for oil palm development (Pirker et al. 2016). Costa Rica's palm oil industry is emerging, with 77,750 ha harvested in 2014 (FAO 2014). Its production is increasing steadily annually, albeit at a slower pace than some nearby countries with similar mammal assemblages (e.g., Brazil, Columbia and Ecuador). I sampled both industrial and smallholder oil palm plantations in Costa Rica for their connectivity value, amongst other land covers, in a biological corridor spanning approximately 700 km^2 in Costa Rica (Chapters 5-7).

Third-Party Certification

The rapid expansion of wood pulp and palm oil commodities and associated deforestation has led to a push by the international community for sustainability in these industries (Hatanaka et al. 2005, Butler and Laurance 2008, Bartley 2003, 2007, Yaap et al. 2010). National policies to support forest conservation outside of protected areas and riparian zones are rarely in place in developing countries. Third-party

sustainability certification standards are trying to fill this gap (Bartley 2003, 2007, Hatanaka et al. 2005) by requiring certified producers to maintain areas of high conservation value, such as important biological corridors, within production landscapes. The Roundtable on Sustainable Oil Palm (RSPO) and Forest Stewardship Council (FSC) are two of the most widely used certification schemes for these commodities. Both rely on the HCV approach to identify areas that should be set aside to protect important conservation values, such as threatened species as per the International Union for Conservation of Nature (IUCN) Red List of Threatened species and their habitats (RSPO 2013, FSC 2015, HCVRN 2013). This thesis research is intended to benefit HCV practitioners and scientists—evaluating evidence of mammal use of biological corridors and non-forest habitats in fragmented landscapes and insight into the efficacy of widely used rapid-sampling methods.

Study Areas

Sumatra, Indonesia

Initial fieldwork for this dissertation was conducted in Riau Province of Sumatra, Indonesia (Figure 1.1), an island with amongst the largest number of threatened terrestrial mammal species in the world (Pimm et al. 2014). Research was undertaken at an *Acacia* pulp-fiber plantation owned by Asia Pacific Resources International Limited (APRIL). My initial research plan was to conduct extensive field research solely in *Acacia* plantations in Riau. This plan was altered when the company abruptly withdrew from the research agreement after the pilot phase of the study due to my primary supervisor criticizing their clearance of natural forests on Australian national television (Brown 2011). Chapters 3 and 4 therefore only include data from a six-month pilot phase, where sampling took place in the riparian forests of one plantation, and do not include sampling of the extensive *Acacia* stands (matrix) or additional plantations for comparison.

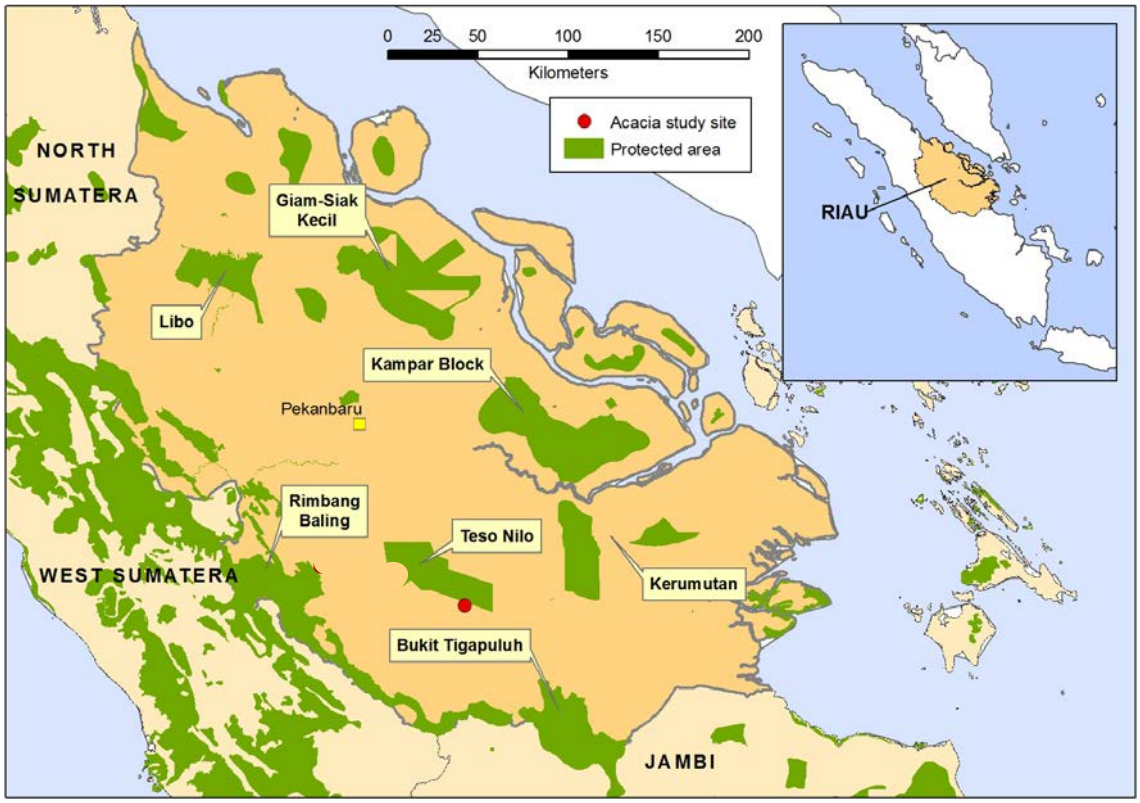

Figure 1.1 Location of the *Acacia mangium* plantation study site, adjacent to Tesso Nilo National Park, in Riau Province, Sumatra, Indonesia.

Osa Peninsula, Costa Rica

After being excluded from the first research site, I decided it was too risky to rely on industry and potential internal company politics to complete my research. I therefore relocated to a site on Costa Rica's Osa Peninsula (Figure 1.2) where the Costa Rican government body responsible for managing national conservation areas, Sistema Nacional de Áreas de Conservación (SINAC), was very supportive of research regarding connectivity between Corcovado National Park and Piedras Blancas National Park via the Osa Biological Corridor. I successfully completed a comprehensive six-month study of habitat use, species distribution and connectivity in this corridor for large mammals, detailed in Chapters 5-7 of this thesis.

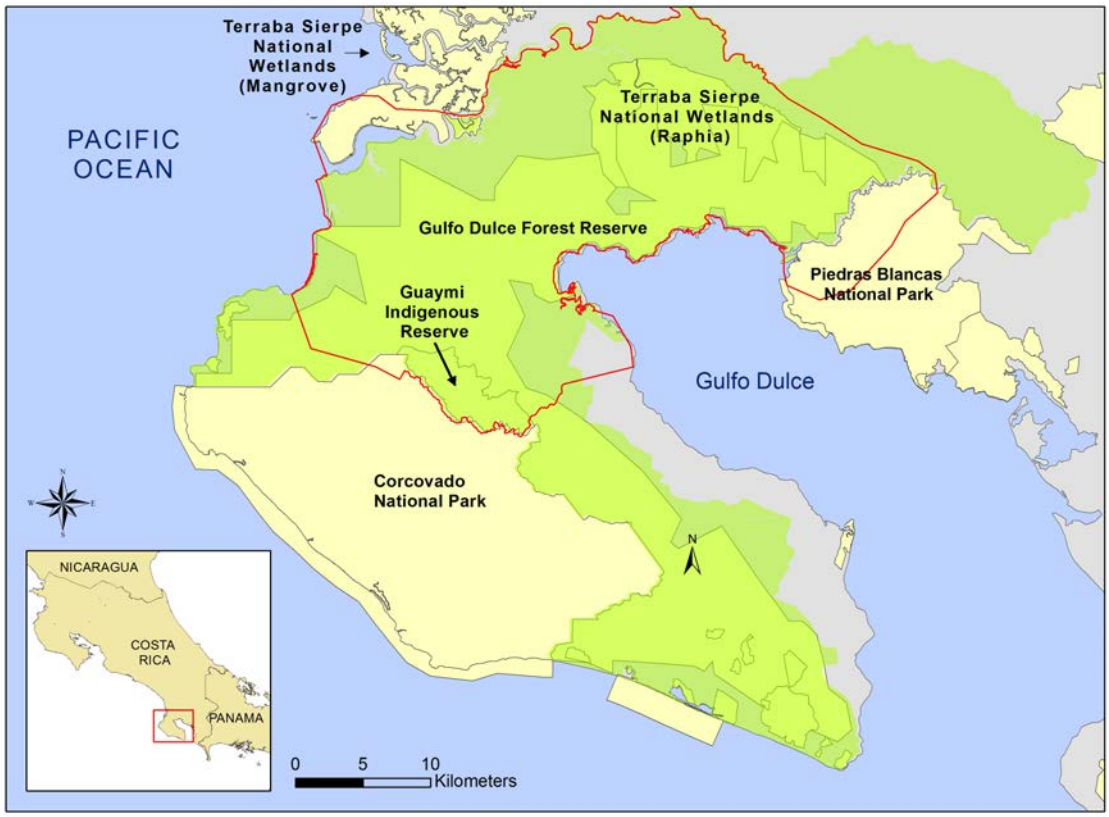

Figure 1.2 Location of the Osa Biological Corridor (green transparent layer) and study area (red outline) located in Puntarenas Province, Costa Rica. Protected areas are colored in light yellow, with those referenced in this thesis labeled.

Chapter 2 A review of tropical forest corridor literature

This chapter is based upon a paper in preparation:

Yaap, Betsy [a], William F. Laurance[a] and Susan G. Laurance [a]. In prep. Journal to be determined.

[a] Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia.

Statement of contribution of others:

Laurance, W.F. and Laurance, S.G. reviewed this chapter and provided input.

Introduction

Deforestation and habitat fragmentation in humid tropical rainforests continue to be a major threat to biodiversity conservation (Laurance 1999, Hansen et al. 2008). Biological corridors are a popular conservation strategy thought to enhance connectivity, in turn reducing extinction risk, in fragmented landscapes (Wilson and Willis 1975, Diamond 1975, Bennett 2003, Hilty et al. 2006). There is an extensive body of literature on corridors and connectivity, yet the vast majority of scientific research into corridors has taken place in temperate regions (see reviews by Debinski and Holt 2000, Beier and Noss 1998, Bennett 2003, Gilbert-Norton et al. 2010). As popular as corridors have become in conservation initiatives worldwide, the principles of corridor design developed based on research from temperate regions have yet to be collectively analyzed for tropical regions to determine if the same principles hold true. Concerns have also been voiced about corridors in general, mostly over the lack of scientific evidence on the success of corridors in maintaining connectivity, their potential for becoming a population 'sink' and facilitating spread of disease and invasive species, and questions of the cost-benefit trade off (i.e., Are there better uses for limited conservation resources?) (e.g., Hess 1994, Simberloff and Cox 1987, Simberloff et al. 1992, Krewenka et al. 2011, Procheş et al. 2005).

In this review of tropical forest corridors, I focus on the first of these concerns: the scientific evidence supporting the ability of forest corridors "to assist the movements of animals" and/or "maintain the continuity of species populations and ecological processes in the face of habitat change" (Bennett 2003). I begin by providing a brief summary of conclusions on corridor design drawn from literature largely informed by studies in temperate regions. I then review published, peer-reviewed studies undertaken in tropical forests to identify (1) the extent and type of corridor research undertaken, and (2) findings on corridor usage for mammals.

Methods

Searching the ISI Web of Science (ISI 2017) using the keywords 'corridor' and 'wildlife', I identified the most frequently cited journal articles on the topic and review articles to

identify key corridor design considerations. I also read two books on corridors, Bennett (2003) and Hilty (2006), and the United States Department of Agriculture's Handbook on conservation corridor planning (United States Department of Agriculture [USDA] 2004). From these I created a list of design elements to use in my review of tropical corridor literature.

I then searched the ISI Web of Science (ISI 2017) for papers with the following search criteria for all years through to June 2017: Topic = *corridor* AND *tropic*.* (The star truncation allowed inclusion of any additional characters that may come after the word *tropic*—i.e., tropical and tropics). This resulted in 612 papers. I refined the results by restricting the search to the following subject areas: Ecology, Environmental Sciences, and Biodiversity Conservation; reducing the results to 298 papers.

I limited the review to studies that investigated the use of linear forest habitat connected to a larger patch of forest habitat. This included 'true' corridors (linear habitat connecting two larger patches of habitat through a matrix of non-habitat), linear remnant forests (extending into a matrix, away from a patch of habitat, but not connected to a second patch), and living fences (when they are connected to habitat patches). I removed studies investigating stepping-stones as corridors for volant species, wind corridors, road corridors, and migratory bird corridors, as well as corridor modeling papers and phylogeographic and aquatic studies. Tropical corridor studies in savannah woodland landscapes (e.g., elephant corridors in Kenya and Botswana) were also excluded.

I identified and included additional empirical, tropical forest papers that fit the above criteria, but were not identified in the ISI Web of Science search through citations in the papers identified in the initial search and using Google Scholar. This resulted in a final sample size of 56 papers distributed across 22 journals.

Trends in corridor studies were summarized by year, region, corridor type, study design (experimental versus observational; demographic or pure movement; genetic, radio telemetry, mark recapture or occupancy), and taxonomic group. To summarize each mammal paper (excluding bats) I recorded the following information: whether the structural design features identified in the initial corridor design review was a

variable in the study, and if that design feature influenced use of the corridor by the species studied.

Results

Corridor Design

Just as forest fragmentation occurs at varying patterns and scales, so do corridors designed to maintain connectivity in fragmented landscapes. There are many ways to categorize conservation corridors based on structure and function, and terminology is varied, often causing confusion (Hess and Fischer 2001). Bennett (2003) identifies five types of 'linkages' which exemplify common types of conservation corridors. These categories will be used for this review.

1. Landscape linkages between reserves or large natural areas, generally aimed at maintaining a complete representation of biodiversity in the region (e.g., my Costa Rica study site discussed in Chapters 5-7).

2. Linked systems of habitat at the regional scale, which are exemplified by highly fragmented, agricultural landscapes, following the patch-corridor-matrix paradigm of landscape ecology (Forman and Godron 1986), whereby reserves (patches) are intentionally linked by a network of linear vegetation (corridors) of natural forest or planted trees along rivers or roads, in a matrix of pasture or agricultural land. Such systems can extend countrywide and are best known to developed countries and temperate regions.

3. Linkages in forest conservation and management, typified by production forest landscapes where remnant natural forest strips are embedded in a patchy matrix of production forest at different stages of regrowth (e.g., my Indonesia study site discussed in Chapters 3-4).

4. Linkages for the conservation of large mammals aim to maintain connectivity along migration routes (e.g., elephants) and populations that may be unviable due to isolation and small numbers (e.g., giant panda and Sumatran rhino). Such linkages usually entail connecting reserves and large natural areas, but do not necessarily

aim to maintain a complete representation of regional biodiversity, but rather enable passage of particular species, often through non-protected lands.

5. Local networks of linear habitat in agricultural landscapes. These are typical of tropical landscapes, often in the form of living fences, windbreaks, and riparian forests (usually retained to meet legislative requirements). This category differs from Category # 2 (above) in scale and that these networks are not part of a large, active, landscape connectivity management approach, but rather relics of habitat conversion. Corridors in these systems are often highly fragmented.

Structurally, corridors can fall into the classic definition of a 'true corridor', where two large habitat fragments are connected by a linear strip of habitat, or be made up of 'stepping stones' where smaller fragments (patches) are located close enough together to provide connectivity between two larger fragments. If a 'true corridor' has numerous gaps, it may be viewed more of a stepping stone structure. To make a clear separation from the extensive body of forest fragmentation literature, this review focuses on corridors of linear structure. In real landscapes, such 'corridors' may be peninsular shaped, dead-ending in a matrix of non-forest, but still provide valuable information on species willingness to use such linear structures (e.g., Chapter 4).

Ideally the structure of a corridor is defined preemptively and is designed with a particular function in mind, but corridors are more often designed as a response to threats to the last remaining areas of connectivity in a natural landscape or by piecing together fragments of remnant natural forest. Nonetheless, functionality is central to corridor design for biodiversity conservation and is the first step in corridor design: What is the biological purpose of the linkage? (Bennett 2003). Depending on the intended purpose or function, and social, economic and political factors (especially land tenure), the design and management of corridors will need to be determined on a project-by-project basis (United States Department of Agriculture [USDA] 2004). As Bennett (2003) states, it is "neither possible nor desirable to provide specific uniform guidelines for the design and management of habitat links," rather it is "more useful to discuss biological issues that have a strong influence on the way linkages function and their effectiveness."

This said, there are a number of corridor design considerations repeated throughout the corridor literature that are expected to influence corridor function, as well as a couple of rarely mentioned ones. They include corridor width, length, and habitat quality; matrix permeability; direct connectivity; proximity to anthropogenic disturbances; multiple levels of ecosystem connectivity; and presence of alternative pathways and habitat nodes (Table 2.1). Depending on the functional goal, corridor design will likely be based on (1) species-specific habitat use and movement patterns, or, in the case of larger landscape linkages, on (2) maintaining multiple levels of ecosystem connectivity. Gregory and Beier (2014) provides further division, identifying seven corridor goals, appropriate response variables for each goal and sample efficacy and effort associated with each.

Table 2.1 A list of structural components, placement considerations and ecological factors to be considered in the design of conservation corridors.

Structure and placement	Considerations	Select References
Species specific ecology, habitat use and movement	• Life history • Habitat needs • Generalist vs. specialist diets • Passage species vs. corridor dwellers • Nesting & denning features • Seasonal migrations • Social organization • Age and sex of dispersing individuals • Sensitivity to disturbance • Elevation limits	Chetkiewicz et al. (2006), Beier and Loe (1992), Lindenmayer and Nix (1993), Beier and Noss (1998), Ricketts (2001), Hess and Fischer (2001), Collinge (1996), Hilty et al. (2006), Bennett (2003), United States Department of Agriculture [USDA] (2004), Beier et al. (2008), Laurance (2004), Debinski and Holt (2000)
Width	• Generally, wider is better than narrow • How is the species affected by edge effects? • How will the longevity of the corridor be affected by edge effects? • If a corridor dweller, width should be wider than the species' home range	Beier et al. (2008), Beier and Noss (1998), Bennett (2003), Laurance (2004), Ricketts (2001), United States Department of Agriculture [USDA] (2004), Hess and Fischer (2001), Hilty et al. (2006)
Length	• Generally, the longer the corridor the wider it should be	Lindenmayer and Nix (1993), Beier and Loe (1992), Beier and Noss (1998), Ricketts (2001), United States Department of Agriculture [USDA] (2004), Laurance (2004), Collinge (1996), Bennett (2003), Hilty et al. (2006)
Matrix use/ permeability	• Ability to use the matrix influences corridor and overall landscape use • Some species will use the matrix	Beier et al. (2008), Beier and Noss (1998), Bennett (2003), Collinge (1996), Laurance

Structure and placement	Considerations	Select References
	only if it is in proximity to a corridor (or natural forest fragment) • For some species, the matrix can serve as habitat and a corridor in its own right	(2004), Lindenmayer and Nix (1993), Ricketts (2001), United States Department of Agriculture [USDA] (2004), Hilty et al. (2006)
Habitat quality	• Varies based on species-specific needs • Vegetation quality: availability of particular food species • Often translated into structural components of vegetation in corridor studies: e.g., forest height, canopy cover, basal area, ground cover • Indicators of disturbance • Presence of invasive species	Beier and Loe (1992), Lindenmayer and Nix (1993), Beier and Noss (1998), United States Department of Agriculture [USDA] (2004), Laurance (2004), Bennett (2003), Hilty et al. (2006)
Connectivity	• Number and length of gaps between corridor and patch • Degree of isolation for patch or large forest • Distance to 'mainland' or nearest large patch of forest (in some studies measured as distance along the corridor)	United States Department of Agriculture [USDA] (2004), Rouget et al. (2006), Lindenmayer and Nix (1993), Hilty et al. (2006), Beier and Noss (1998), Bennett (2003)
Alternate pathways	• Number of corridors present between patches being connected	Bennett (2003)
Nodes	• Presence of wider habitat nodes in the corridor as temporary stopping points during passage	Bennett (2003)
Anthropogenic disturbances	• Hunting • Transport corridors (roads, trains, canals, etc.) • Settlements • Logging or other harvesting • Recreational use	Beier and Noss (1998), Ricketts (2001), Laurance (2004), Bennett (2003), Beier and Loe (1992), Hess and Fischer (2001), Collinge (1996), Hilty et al. (2006)

Extent and types of tropical forest corridor studies

Of the more than 298 papers reviewed, the vast majority were not biological studies of tropical forest corridors. The results embodied the multiplicity of definitions the term corridor embodies to different people (Beier and Noss 1998, Bennett 2003, Hess and Fischer 2001), with, for example, 'wind corridors', 'road corridors', 'stream corridors' and bird 'migratory corridors' allowing inclusion into the search results. Studies that did not meet the review criteria, but were relevant to the topic could be categorized as follows: (A) studies that were not corridor studies, but provided animal movement or behavioral information that the author(s) thought important by the authors to inform

corridor design, (B) studies recommending a corridor for a particular species or landscape, (C) studies on invasive species use of corridors, (D) corridor modeling and/or mapping studies, and (E) studies that didn't fall comfortably into any category, but that shed some light onto the question of effectiveness of tropical forest corridors. Of interest, but not reviewed in this study is a large, emerging body of literature on modeling corridors, increasingly using empirical data (Zeller et al. 2012, Abrahms et al. 2017, and, for example, Brodie et al. 2015).

Year

There is a clear pattern of increasing research interest in linear forest habitat as corridors in tropical landscapes over the past almost 30 years: 10 studies from 1990-1999, 22 from 2000-2009, and already 24 studies from 2010-June 2017.

Region

There is a distinct difference in regional engagement in tropical corridor studies (Table 2.2), with Latin America leading the way in tropical corridor studies with 35 studies from the region, mainly in Brazil, Costa Rica and Mexico. Eight studies were from Australia; seven of which were conducted in the Atherton Tablelands of Queensland. Studies in Asia, Africa and Pacific islands were the least prevalent. This does not necessarily reflect a lack of interest in corridors in these other regions. Large mammal corridors in non-forest and non-tropical regions of Africa are widely accepted and applied as a conservation tool in east and South Africa (e.g., Newmark et al. 2010, Thomas et al. 2008, Kikoti et al. 2010, Rouget et al. 2006) and the studies reviewed here show studies of forest corridors in central and west Africa as well as Madagascar. Research by Ramiadantsoa et al. (2015) in Madagascar is unusual in its broad scope, investigating use of a large-scale corridor (95 km in length) connecting two national parks by five taxonomic groups.

Although only seven studies from Asia are included in the review, there is a regional interest in corridors. For example, wildlife managers and researchers in Malaysia and Indonesia are investigating wildlife use of riparian forests in oil palm plantations and an experimental design project in Sabah is currently being established, with fragment size, isolation and corridors central to the study design (Ewers et al. 2011, Gray et al.

2016, Gray et al. 2014). More research into linear forest remnants in agricultural landscapes will likely emerge from Malaysia and Indonesia in the near future with the high rate of ongoing fragmentation for palm oil and pulp and paper industries and a scientific debate over 'designer landscapes' (Koh and Wilcove 2008, Koh et al. 2009, Struebig et al. 2010). Corridors for large mammals are also well known to the region. India and Sri Lanka have a history of elephant corridors (Johnsingh et al. 1990, Johnsingh and Williams 1999). Environmental non-government organizations also frequently include the corridor concept in their regional approach to conservation. For example, in Sumatra and mainland Southeast Asia there is a strong focus on corridor connectivity for tigers (Lynam et al. 2006, Panthera 2012).

The prevalence of studies in Latin America, especially Brazil, is not surprising due to the large quantity of tropical forest and high level of fragmentation paired with laws on maintaining riparian forest buffers and a well-educated pool of scientists in the region. This has led to a large number of studies on linear forest remnants as corridors. Latin America also has a very strong movement towards creating landscape linkages to connect protected areas and preserve large-scale ecosystem processes. This is particularly clear in Costa Rica, where such corridors have been identified across the country. Scientific studies on the success of these large-scale corridors have not been forthcoming, but corridors remain a popular conservation tool in the region. Most notable in Latin America is the Mesoamerican Biological Corridor (DeClerck et al. 2010, Diaz-Gallegos et al. 2008), stretching from Mexico all the way through to Panama, connecting nodes of protected areas. The jaguar (*Panthera onca*) a wide-ranging, near threatened species, has also been a focus for regional corridors, with Rabinowitz and Zeller (2010) mapping a network of corridors for the species: five corridors ranging from 2-1,102 km long in Mexico and Central America and 39 corridors in South America ranging from 12-1,607 km in length.

Australia has been one of the leaders in corridor research with much of its research taking place in temperate regions. With limited tropical rainforests, 3,280,000 ha, making up only 2% of the country's forests (ABARES 2012), Australia provides a disproportionate high amount of empirical studies on tropical forest corridors in comparison to other regions.

Table 2.2 Geographical location of studies included in the literature review.

Region	Number of studies	Countries
Asia	7	Malaysia (3), Indonesia (2), Singapore (1), India (1)
Australia	8	Atherton Tablelands, Queensland (7), Northern Queensland (1)
Latin America	35	Brazil (20), Mexico (7), Costa Rica (7), Puerto Rico (1)
Africa	4	Madagascar (2), Ghana/Côte d'Ivore (1), Cameroon/Central African Republic/Republic of Congo (1)
Pacific Islands	1	Hawaii (1)

Corridor type

Of the five types of conservation corridors, or linkages, identified, Category 5 (local networks of linear habitat in agricultural landscapes) are the most prevalent in the tropical studies reviewed. Corridor studies in forestry landscapes (Category 3) are less prevalent, but also relatively common.

As described in the region section, there are also examples of conservation initiatives to establish linkages between reserves and large natural areas (Category 1) and for the conservation of large mammals (Category 4); the latter often the impetus for such large-scale initiatives in tropical countries.

Linked systems of habitat at the regional scale (Category 2) are the least prevalent in the tropics, with Singapore the only solid example appearing in the published literature (e.g., Sodhi et al. 1999). This is not surprising due to the highly developed state of the island and economic status of country.

Study design

The vast majority of tropical corridor studies are observational (not experimental) in design (Appendix A). Only two experimental studies, both in Costa Rica, one on army ants (Meisel 2006) and another on hummingbird (Kormann et al. 2016), used an experimental design, while the other 55 studies were observational. Beier and Noss (1998) describe the difficulty in designing and conducting experimental corridor studies, noting the ethical issues of destroying connectivity. It is therefore not

surprising to find all but two of the studies reviewed experimental in design and those that did working at very small scales.

Secondly, 50 of the 56 studies were based on demographic parameters (e.g., occupancy, abundance, diversity, activity level) rather than documenting movement across the landscape (e.g., via radio telemetry or GPS tracking). Of the six studies that documented movement, five were bird studies and one an ant study (Appendix A). Again, this is not surprising because of the associated time and/or cost and logistical difficulty in trapping some species. Permits can also be difficult to obtain to capture, sedate and collar protected species—often the species of interest for corridor design. This said, Horskins et al. (2006) and Beier and Noss (1998) note the risk in assuming that use of a corridor implies connectivity of populations in patches, so movement and genetic studies are preferable to observational studies using demographic parameters as the response variable. For example, in African wild dogs, movement behavior has been shown to be a better predictor of connectivity than resource selection (Abrahms et al. 2017).

Genetic studies are on the forefront of corridor studies with their ability to provide more solid scientific evidence of connectivity. Time lag in population genetics can be an issue, but some studies are now using genetic markers to identify individuals (e.g., Borthakur et al. 2011), making it possible to determine (from fecal or hair samples) if the same individual is using the two areas being targeted for connectivity. In the current review, only 3 studies used genetic analyses—on small mammals, frog and trees (Appendix A). It is likely that such research will become more prevalent in the future.

Mark recapture studies are also being used to identify movement across landscapes. Using camera traps, species with distinct features (e.g., tiger or jaguar coat patterns) can be identified to the individual and shed light on corridor use and connectivity. Although commonly used in felid research, no published mammal studies using this technique appeared in the literature search for this review. Mark-recapture techniques were used in some bird, small mammal and beetle studies—mostly to distinguish between unique captures at individual traps. Only one bird study used marked,

translocated birds to identify movement along linear remnants between forest fragments in the landscape (Ibarra-Macias et al. 2011b).

Taxonomic Group

Mammals and birds were the most frequently studied taxonomic groups—22 and 20 studies focusing on the taxonomic groups, respectively (Table 2.3 and Appendix A). Medium and large mammals were the most frequently studied mammals (n = 11), followed by bats (n=6) and small mammals (n=6). Invertebrate studies, mostly ants and dung beetles, were also prevalent (n=10). Plants, amphibians and reptiles were the least frequently studies. The prevalence of mammal and bird studies is not surprising because these taxonomic groups are frequently the target of conservation initiatives and arguably the best understood of tropical rainforest fauna.

Table 2.3 Taxonomic groups surveyed in studies included in the literature review. Some studies surveyed more than one taxonomic group.

Taxa	# of papers
Mammal	22
Bird	20
Plant	8
Reptile	2
Amphibian	4
Invertebrate	10
Total	84

Mammal studies

Large mammals: Study-by-study

Fourteen large mammal studies were reviewed—Australia (4), Asia (4), Africa (3), and Latin America (3)—and are summarized below (Table 2.4).

Australia

Several studies on arboreal marsupial use of remnant riparian forests embedded in a cattle pasture matrix have been published from the Atherton Tablelands of Queensland, Australia (Laurance et al. 2008, Laurance 1990, Laurance 1991, Laurance and Laurance 1999). These corridors align closely with corridor design Category 5

(described above), a local network of linear habitat in agricultural landscapes as a relic of habitat conversion.

Use of ten forest fragments (patches), three corridors and seven control sites by five arboreal marsupials was compared in Laurance (1990). The corridors were 10-50 m wide strips of secondary riparian vegetation that connected fragments to the continuous natural forest habitat. He found that extinction proneness of the five species studied was related to their ability to use secondary forest along riparian forest corridors, not rarity of a species in continuous tracts of forest. Fragment area and isolation explained most of the variation in species richness in forest fragments. Elevation had a clear influence on density of some species.

The broader assemblage of rainforest mammals from the same study sites as above is described In Laurance (1991). This study also presents the presence and abundance of 16 non-volant mammals, he identified life-history traits that enable species to use fragments and corridors. He found that species that tolerate or can exploit the matrix, use edge habitat, or secondary regrowth in the matrix are much more likely to use corridors and inhabit fragments connected by these corridors. Nine species were recorded using the corridors and were also present in the connecting fragments: two arboreal possums, a tree kangaroo, a carnivorous marsupial, and five rodents. The mammals most vulnerable to extinction in fragments were ones unwilling to use secondary vegetation and the corridors: including two possums, a primitive rat-kangaroo, and three carnivorous marsupials. He concludes that such species would require much wider corridors of primary forest to maintain connectivity in the landscape. He also emphasizes that reforestation of forest corridors is not a viable alternative for maintaining connectivity in the landscape because the pace of species extinction in these fragments is faster than the possible establishment rate of mature-phase forest corridors.

The “effects of corridor width, height, isolation, elevation and floristic composition” on arboreal marsupial use of linear remnant forests was also investigated by Laurance and Laurance (1999). Spotlighting along transects of 36 linear remnant forest in three categories of forest type and three categories of isolation (isolated, linked to forest fragment of >5 ha, linked to forest fragment of >3000 ha), they identified six species

and found that the species varied in their willingness to use corridors of varying characteristics. They concluded that "linear forest remnants that are floristically diverse … and at least 30-40 m wide, can function as habitat and probably movement corridors for most arboreal mammals" in the region. They identified one species, the lemuroid ringtail (a forest-dependent, habitat specialist) that is expected to need a primary forest corridor of at least 200 m wide for use or passage.

In Laurance et al. (2008), they returned to resurvey the same study sites from twenty years previous and found that fragment connectivity continues to play a role in species richness. The study showed that the size of discontinuities in stream corridors and level of fragment isolation from other forest areas explained up to 56% of variation in species richness. The comparison over the twenty-year time period allowed them to confirm their previous predictions, a trend of corridor and matrix using species continuing to survive in fragments and corridor-avoiding species declining or disappearing. They suggest that the most sensitive species are more likely to traverse corridors that are short in length, and advise that the best corridors for vulnerable mammals in tropical Queensland will be >200 m wide, continuous (without breaks), composed of primary forest vegetation (or mature, species-rich secondary forest), and will occur at an elevation of >750 m.

Asia

Only four published studies from tropical Asia were found to fit the review criteria, three of which took place in *Acacia* plantations: a study of primate use of riparian forests in Riau, Sumatra (Nasi et al. 2008); my camera trapping study of medium and large mammal use of riparian linear remnants, also in Riau (Chapter 4); and a camera trap survey of riparian, secondary forests and *Acacia* in Malaysian Borneo (McShea et al. 2009). The corridors in these three studies align with Category 3: Linkages in forest conservation and management.

In Riau, Sumatra, Nasi et al. (2008) tested whether primate occurrence and species richness in remnant natural forest in an *Acacia mangium* plantation was influenced by connectivity to large tracts of natural forest, riparian corridor width, distance to roads, crown closure, the age and height of the surrounding *Acacia* stands, and structure of

remnant forest. They sampled primates in 100 -1 km^2 grid cells that included riparian forest corridors embedded in three *Acacia mangium* plantations. The majority of the riparian corridors were <50 m wide, but ranged up to more than 150 m in width. Most were peninsulas, connecting to the national park or other small conservation areas and dead-ending in the plantation, or disconnected linear forest remnants. The corridors were multiple kilometers long. Seven species of primate were positively identified: three gibbons, two macaques, and two langurs. Primates were only found in 30 of the 100 cells sampled, and only found in riparian forests that connected to larger patches of forest (>3,000 ha) or to the neighboring national park. However, 45% of connected riparian forests were still absent of primates. Age of the surrounding matrix (*Acacia*) was not found to influence primate occupancy. Abundance and species richness were significantly higher in cells that (1) had 20-30% of the cell as forest, (2) greater crown closure, and (3) were less disturbed (more distant to roads and experienced less logging). With regard to primate diet and vegetation, diets vary between primate species, and riparian forests in this study (which are remnant primary forests) are thought to offer the wide variety of food sources necessary to maintain the varying needs of each species. The authors highlight the importance of connectivity to source habitat, habitat quality (crown closure, disturbance from logging and roads), and percent of natural forest habitat in the overall landscape (ca. 30% in this study) for corridors to maintain a connectivity function in the landscape.

In my linear remnant study in Sumatra (Chapter 4), camera traps were used to detect mammals at 57 sites to assess the effects of corridor-design and land cover covariates and species behavioral traits on mammal habitat use of four linear riparian forests. I recorded 17 species (including one IUCN Critically Endangered, two Endangered and four Vulnerable) in riparian forests inside the plantation, including the Sumatran tiger (*Panthera tigris* sumatrae), Malay tapir (*Tapirus indicus*) and sun bear (*Helarctos malayanus*). Some threatened species were detected in the park buffer zone. Species varied in their responses to riparian forests, but distance to the national park, remnant width, and percent forest cover around the camera sites were common predictors of remnant use. Many mammal species used riparian forests regardless of whether they were surrounded by intact *Acacia* forests or recently cleared land. The study

concluded that linear remnant riparian forests ≤ 200 m in width can facilitate local (< 4 km) movements of many large mammal species in Sumatra, but wider riparian remnants would likely be more effective at promoting mammal movements over longer distances.

Another survey in an *Acacia* plantation in Sarawak, Malaysia (McShea et al. 2009) surveyed riparian forest corridors in a study focused on large terrestrial mammal use of *Acacia* and the influence of secondary forest and corridors on its use. Of the 644 km2 study area, approximately 47% of the area was *Acacia* of 1-7 years old, 31% secondary forest in the form patches (122 m2–97.4 km2) and riparian forest corridors (10-100 m wide), and the remainder shifting agriculture. Twenty-seven species were identified at 212 sample sites, divided into three categories: young *Acacia*, old *Acacia* and secondary forests. Arboreal mammals were reportedly absent from the secondary forest before conversion to *Acacia*, and not identified in the study. Five large mammals were only identified in secondary forest (an otter, lesser mousedeer, clouded leopard, long-tailed macaque and long-tailed porcupine), but it is unclear whether these detections were in corridors or secondary forest fragments. Four species were only found in relatively close proximity to secondary forest: sun bear (*Helarctos malayanus*), common porcupine, (*Hystrix brachyura*) mousedeer (*Tragulus* spp.), and pig-tailed macaque (*Macaca nemestrina*). Unfortunately, the study results did not distinguish between secondary forest in patches and corridors, grouping the two in a single 'secondary forest' category for analysis. The authors do state that they "did not detect an obvious use by terrestrial mammals of the thin corridors of secondary forest maintained along streams." The study concludes that mature *Acacia* stands (4-8 years old) are capable of serving as a corridor between fragments of secondary forest, noting that species detections in secondary forest were significantly higher than that in *Acacia*, but species richness was not.

Asian elephant (*Elephas maximus*) use of five elephant corridors in India (two of which were in tropical regions) were summarized in Johnsingh and Williams (1999). Corridors described ranged from 0.5-3 km wide and 3-13 km long. The corridors in this study are most closely aligned with Category 4: Linkages for the conservation of large mammals along migration routes, but also align with Category 1: Landscape linkages. The authors

emphasize the influence of anthropogenic disturbances in determining elephant use of corridors. Railways, roads, a channel, land conversion to agriculture and natural features of the landscape (e.g., steep limestone cliffs and large boulder formations along a river) were identified as barriers to corridor use. In two cases only bulls were still known to use the corridors due to difficulty in navigating road and channel barriers. Of the two corridors located in the tropics, a 13 km corridor was no longer in use by elephants due to a railway, road and agricultural encroachment. The other, 7-km long and varying from 0.5-3 km wide, was still in use but under imminent threat from development.

Africa

Parren et al. (2002) identified three regional corridors thought most suitable for forest elephants (*Loxodonta africana cyclotis*) in the border region of Côte d'Ivoire and Ghana. These corridors could be considered landscape linkages (Category 1), but more closely reflect local networks of linear habitat (Category 5) because they exist in a highly fragmented landscape. Corridor identification was based on presence or potential establishment of a 0.5–1.5 km wide corridor (based on current land cover and farmer attitudes towards a corridor), elephant preferred food plants, water availability and human population pressures. Field surveys were undertaken to identify current distribution of elephants in protected forests and use of four 'shelterbelts', 1.5 km wide and up to 20 km long forested wind and erosion breaks maintained in the Ghanan landscape since the mid 1930's. Of the four shelterbelts, only two were true corridors, while the others were peninsulas. Field surveys revealed only one of the corridors had elephant use across the entire length (<10 km) of the corridor; the only corridor connecting two forest patches occupied by elephants. The other 'true' corridor (<15 km long) only had one patch occupied by elephants, and evidence of elephant use of this corridor was only found on the side of the corridor connected to this patch. The two peninsular corridors were adjacent to occupied patches. One seemingly had complete connectivity and elephants were reported to use areas 4-5 km into the <20 km long corridor, while the other had a gap between the corridor and patch and elephant use was not documented in the <15 km long corridor.

Forest elephant (*Loxodonta africana cyclotis*) corridors along a highly traveled river bisecting the Sangha Trinational Park in central Africa (on the border of Cameroon, Central African Republic and the Republic of Congo) were identified and described by Weinbaum et al. (2007), who surveying two 30-km transects 500 m from the river (on either side) they used dung counts to estimate elephant density. As with the elephant study in India, the corridors in this study are best described as Category 4: Linkages for the conservation of large mammals along migration routes, but also align with Category 1: Landscape linkages. Mapping density gradients along the rivers, 'corridors' of more intensively used areas were identified. Four locations of medium to high intensity were identified, each c. 2-5 km wide. Ecological and anthropogenic determinants were analyzed, revealing previously known patterns of elephant behavior—preference for secondary vegetation (and other known preferred food habitats) and avoidance of areas with human activities. They also detected a significant difference in density on opposite sides of the river, which they attribute to previous and current land management (logging and disproportionate anti-poaching efforts).

Ramiadantsoa et al. (2015) studied the functionality of a large 95-km long forest corridor for connecting two large national parks in the southeastern escarpment of Madagascar for five taxonomic groups, including lemurs. The corridor in this study is a good example of Category 1: Landscape linkages between reserves or large natural areas. Fifteen sites (eight in the corridor) were surveyed using line transects, identifying 12 lemur species. Average species richness was found to be highest in one of the national parks and equal in the corridor and the second national park. Only nine species were present in all three categories (both national parks and the connecting corridor) and none were unique to the corridor. It was acknowledged that habitat quality and preference influence species distribution, for example, with bamboo prefer bamboo stands that are more abundant in degraded habitat in the corridor. Separate genetic studies on the black-and-white ruffed lemur (*Varecia variegate*), an intact forest specialist, in one of the national parks have determined that the population is inbred, showing that the corridor unlikely provides connectivity for this species, and it might also be the case for other species, particularly species that avoid gaps.

Latin America

A study of mammal (and bird) use of riparian, linear forest remnants in a cattle pasture matrix (Category 5: Local network of linear habitat in agricultural landscapes) in Brazil's southern Amazon (Lees and Peres 2008) compared species richness and composition in 32 linear forest remnants of different width (80-500 m), connectivity (to forest fragments of >200 m) and disturbance levels. Eight of the 32 linear forest remnants (referred to as corridors) were not connected to a forest fragment (i.e., >300 m from the nearest forest patch). An additional 5 riparian forests in large forest blocks were surveyed as controls. All corridors were at least 1,700 m in length. The matrix was not sampled. Using direct observation and track and sign surveys, the study recorded twenty-two non-primate species and five primate species.

Corridor width and quality of forest habitat were both significant predictors of species richness, while mean corridor height and canopy cover were less important, but still significant predictors. Corridor width was not a significant predictor of primate species richness. In connected corridors, patch size and corridor width were the best predictors of mammal species richness, whereas in unconnected corridors, Mauritia palm (an ungulate and primate food source) abundance and corridor height had the strongest effect. Narrow, unconnected corridors typically retained as little as a quarter of the mammal species richness recorded in control sites.

The authors found that mammal use of linear forest remnants is highly species specific (examples from the text summarized in Appendix B), and "encounter rates for most species were lower in corridors than in control sites." They also note that ability to use unconnected corridors is likely closely associated with species ability to use/tolerate the cattle pasture matrix. Overall, the study concludes that, "Narrow and/or highly disturbed riparian corridors retained only a depauperate vertebrate assemblage that was typical of deforested habitats, whereas wide, well-preserved corridors retained a nearly complete species assemblage." The authors also note that corridors <200 m wide were more vulnerable to edge effects and provided no core habitat.

Another study, in the north-eastern Brazilian Amazon, by Barlow et al. (2010), investigated beetle use of linear remnant forests (riparian and terra firme) in a

eucalyptus plantation matrix, with mammal activity as one of the explanatory variables. These linear remnants align with Category 3: Linkages in forest and conservation management. Eight forest strips (half riparian, half terra firme) were sampled. Sample sites in each forest strip (corridor) were stratified into three categories: control (in forest patch), near (at the start of the corridor), and far (terra firme 2.5-4 km and riparian 6-9 km into the corridor). Corridors were 95-300 m wide and up to 9 km long. For mammals, one-kilometer line transects were walked six times (three consecutive days in wet season and dry season) recording direct observations and indirect signs of a species. The matrix was sampled prior to this study (see Barlow et al. 2007). Twenty-four species and one species group of mammals were identified (Appendix B). As the study was focused on beetles, mammal data was only analyzed to compare encounter rates of mammals between the two types of forest (finding no significant difference between encounter rates in terra firme and riparian forests) and isolation treatments— near, far and control sites. They found that encounters were significantly more frequent in corridors than in core forest habitat when pooling the treatments, but no significant difference when analyzed within each forest type (which the authors note may be attributed to the small sample size). They also note that their mammal observations are supported by local hunters which stated that ungulates use the corridors as shelter belts, browsing and foraging in the plantation at night and retreating to the corridors during the day. They note that their results may not reflect that of other agricultural areas as the eucalyptus matrix is used by many forest mammals (Barlow et al. 2007).

In an Amazonian cattle ranching landscape, Zimbres et al. (2017) studied terrestrial mammal use of 38 riparian forest strips and five riparian sites within continuous forest to determine the functional role riparian forests can play in such landscape. The study site is best described as Category 5, a local network of linear habitat in agricultural landscapes. The mean width of the riparian remnants was 215 m and length 1.2 km. They examined the effects of corridor width, corridor habitat structure, and landscape context on mammal species richness, composition, and functional diversity. They found that all three measures were higher in continuous forest (core habitat) than in riparian remnants. Habitat degradation resulted in lower species richness and forest

specialists were more species rich in wider corridors. Species composition shifted to matrix-tolerant species with lower levels of forest habitat specificity as deforestation and forest degradation increased.

Table 2.4 Summary of results from each large mammal study included in the literature review. Results are given for each commonly known corridor design component.

First author & Year	Country	Species	Width/ Length of corridors sampled	Species specific response	Ability to use matrix matters	Habitat quality in corridor matters	Wider corridor > response variable*	Greater level corridor connectivity > response variable*	Core habitat > response variable than corridors*	Distance into corridor affects use	Anthropogenic factors influence use
Laurance 1990	Australia	5 arboreal marsupials	10-50 m wide	Yes	Yes	Yes	NA	Yes	sp. specific response	NA	NA
Laurance 1991	Australia	16 non-volant mammals	10-50 m wide	Yes	Yes	Yes	NA	NA	sp. specific response	NA	NA
Johnsing 1999	India	Asian elephant	0.5-3 km wide; 3-13 km long	NA, but yes for gender specific	NA	NA	NA	Yes – anthropogenic disturbances creating impassible gaps	Yes	NA	Yes, roads, agriculture, irrigation projects, mining, railways, human settlements
Laurance 1999	Australia	6 arboreal marsupials	9-490 m in mean width; 250-1,250 m length	Yes	Stated, from previous work	Yes	Yes	Sp. specific response	NA	NA	NA
Parren 2002	Côte d'Ivoire/ Ghana	Forest elephant	0.5-1.5 km wide; up to 20 km long	NA	Noted that they occasionally raid crops, but generally use forests	Yes, water and food trees	NA	Yes	NA	Yes	Yes, human settlement and farmland
Weinbaum 2007	Cameroon/ CAR/Rep. of Congo	Forest elephant	2-5 km wide	NA	NA	Yes	NA	NA	NA	NA	Yes, settlements, logging, hunting
Laurance 2008	Australia	c.12 spp. non-volant mammals	10-50 m wide	Yes	Yes	Yes	NA, one example provided in support	Yes	Yes	NA, but suggest shorter better	NA

First author & Year	Country	Species	Width/ Length of corridors sampled	Species specific response	Ability to use matrix matters	Habitat quality in corridor matters	Wider corridor > response variable*	Greater level corridor connectivity > response variable*	Core habitat > response variable than corridors*	Distance into corridor affects use	Anthropogenic factors influence use
Lees 2008	Brazil	Diurnal primates and large terrestrial mammals	80-500 m wide; ≥1.7 km	Yes	Stated, but not tested	Yes	Yes	Yes	Yes	? Variable change in sp. rich with distance. Change in sp. comp. not described	Yes, cattle intrusion and distance to urban settlement. No for hunting pressure on large mammals
Nasi 2008	Indonesia	Primates	<50-150 m wide; multiple km long	Yes	NA	Yes	Limited support	Yes	Yes sp. rich, abundance variable by sp.	NA	Yes, roads and illegal logging
McShea 2009	Malaysia	27 terrestrial mammals	10-100 m wide	Yes	Yes	NA	NA	NA	sp. specific response	NA	Yes, distance to settlement
Barlow 2010	Brazil	Mammals – but as part of a dung beetle study	95-300 m wide; up to 9 km long	Yes	Yes	NA for intactness. *Terra firme* and riparian compared. No significant difference in activity level.	NA	NA	No, higher activity level in corridors	NA	Yes, not tested, but stated that hunting less likely to influence mammal activity than management of the Eucalyptus matrix
Ramiadantsoa 2015	Madagascar	12 lemur spp.	Width: 2-50 km; Length: 95 km	Yes	Stated, but not tested	Yes, not tested for lemurs alone but discussed	NA	NA	Sp. richness highest in one core area, but equal in corridor and second core area.	NA	Yes, not tested, but degradation and deforestation acknowledged as influencing factors.

First author & Year	Country	Species	Width/ Length of corridors sampled	Species specific response	Ability to use matrix matters	Habitat quality in corridor matters	Wider corridor > response variable*	Greater level corridor connectivity > response variable*	Core habitat > response variable than corridors*	Distance into corridor affects use	Anthropogenic factors influence use
Yaap 2016	Indonesia	19 medium and large mammals	Width: 80-530 m, avg 100-200 m; Length: 3.75 km and longer	Yes	Yes. Known from McShea et al. 2009 and some sampling this study.	Yes, % forest cover analyzed. Significant positive for 2 spp., negative for one sp.	Yes, but only for 2 spp.	Yes. Only for 1 sp.	Yes, diversity highest in core habitat.	Yes, for 3 spp.	Yes, not tested, but stated that hunting, logging and harvest rotation likely to influence corridor quality
Zimbres 2016	Brazil	25 medium and large mammals	Width: 215 m mean (ranging 40.1–1316.8); Length: 1.2 km mean (ranging 125 m – 8.6 km)	Yes	Yes, species composition shift to matrix-tolerant species when less forest and degraded forest in corridor.	Yes, lower spp. richness	Yes, > spp. rich for forest dependent species with increasing corridor width	NA	Yes, increased sp. richness and functional diversity in core habitat	No effect detected for spp. richness, composition or functional diversity	Yes, cattle intrusion affected the composition of forest-dependent spp.

*Species richness, occupancy, abundance, activity level, etc.

NA = Not addressed in the study

Summary of large mammal studies

Most of the 14 large mammals studies reviewed were multi-species studies; only three were single species, all on elephants. The elephant studies fit the corridor type Category 4: Linkages for the conservation of large mammals, yet two could also arguably be considered Category 1: Landscape linkages. The elephant study in Cote d'Ivoire and Ghana was in a much more fragmented landscape, more closely reflecting Category 5: Local networks of linear habitat. The corridors in these studies were quite wide and long: ranging from 0.5–9.5 km in width and 2-27 km in length, reflecting the habitat requirements of these large bodied mammals and the landscape linkage element of these studies.

The remaining studies reviewed were community studies. Six of the studies took place in pasture/agricultural matrices (Category 5), four were in plantation forests (Category 3) and one, the Madagascar study, was in a landscape linkage (Category 1). Corridor width varied from 9 m to 5 km. Length wasn't always evident, but the shortest corridor reported was 250 m long, with most multiple kilometers long, and the longest 95 km.

All of the community studies reviewed displayed a species-specific response to corridors. Species ability to use the matrix was tested and deemed relevant in six of the studies. Another five studies acknowledged the importance of matrix permeability and factored it into their study, but did not sample the matrix. A further three studies did not acknowledge matrix permeability or sample the matrix.

Habitat quality (intactness) in corridors was included as a variable in ten of the studies, all finding that better habitat quality had a positive correlation the response variables tested, though a species-specific exists. One study acknowledged the issue of habitat quality, but did not explicitly test for its effect, while three others did not address or test for habitat quality in corridors.

Interestingly, only five studies tested the influence of corridor width. This is likely due to limited variability in corridor width in many of the study areas; for example, riparian vegetation that is being maintained at a standard width along rivers to meet government regulations. It may also reflect a lack of sufficient replicates to test for a width effect. Studies that did test width found support for wider corridors. The studies

that did test width were in pasture/agricultural landscapes and plantations. Collectively these studies advocate that wider riparian buffers are better suited to serve as movement corridors and habitat, and that a minimum buffer width of 100m (50 m either side of a river) is necessary to support forest dependent species, but that up to 400m in width is necessary to retain the same species richness of forest dependent species as connected core areas (Laurance and Laurance 1999, Lees and Peres 2008, Nasi et al. 2008, Yaap et al. 2016, Zimbres et al. 2017). Lees and Peres (2008) point out that buffers of < 400m tend to degrade and have depurate bird and mammal fauna. Noteworthy is a study by Bueno et al. (2012) that found that Amazonian understory forest bird communities need approximately 280m wide riparian forest strips, (recommending 400m total to account for edge effects), which falls within the range that studies are identifying for the mammal communities reviewed.

Direct connectivity with core habitat (lack of gaps or distance of gaps) was tested in eight studies. The studies found that greater connectivity of corridors to forest patches had a significant positive influence on the response variables tested. Two studies showed that direct connectivity was only an issue for certain species. Bueno et al. (2012) highlight the importance of additional conservation set asides being placed adjacent to riparian areas to maximize conservation value of riparian forests for birds. Based on connectivity findings for mammal studies, this recommendation would also benefit mammal communities.

Eleven studies compared their response variable(s) between core habitat and corridors, finding varying responses. Three studies found a species-specific response, six found a higher response variable in core habitat, one found abundance to be a species-specific response, while species richness was higher in the core habitat, and the last study found higher activity levels in corridors than core habitat.

Only four studies tested the effect of distance into corridor, with varying results. One study on forest elephants in West Africa (Parren et al. 2002) found distance into corridor negatively correlated with occupancy. In the Amazon, Lees and Peres (2008) found distance to be more variable over a 1 km distance into the corridor. Species richness dropped in corridors as compared to the source forest patch, but fluctuated

with distance. Also in the Amazon, Zimbres et al. (2017) did not detect an effect of distance into corridor on species richness, composition or functional diversity. My study in Sumatra found that distance into corridor had an influence on occupancy for three species, two positive and one negative, while no effect detected for other species (Chapter 4).

Seven of the studies included anthropogenic disturbances (e.g., hunting, cattle grazing, distance to roads and settlements) as one or more of their response variables and all studies found these anthropogenic disturbances negatively correlated with the study response variable(s). Most other studies acknowledged the influence of anthropogenic disturbances, but did not test for them.

Alternate pathways and nodes in corridors (as described in Bennett 2003), but not prevalent in the corridor literature, were rarely acknowledged and not tested in any of the studies reviewed.

Finally, ecosystem connectivity (inclusion of multiple habitats and topographic gradients) was not explicitly mentioned as a goal of any of the large mammal corridors, yet linking protected areas was central to the elephant studies and the Madagascar study – which, in less fragmented landscapes (such as in Weinbaum et al. 2007, and Ramiadantsoa et al. 2015) by scale alone would lead to greater ecosystem connectivity.

Small Mammals: Study-by-study

Six small mammal studies were reviewed—four in Brazil, one in Australia and one in Madagascar—and are summarized below (Table 2.5). All of the studies took place in fragmented agricultural and pasture landscapes, most closely resembling Category 5: local networks of linear remnants, with the exception of the Madagascar study.

In the Atlantic forest of Brazil, Pardini et al. (2005) studied small mammal abundance and diversity comparing 26 sites in continuous forest and 50-80 year old secondary forest fragments. The fragments were located in a matrix of open land consisting of agricultural fields, urban areas, and native vegetation in early stages of regeneration.

Fragments were divided into three size categories: small <5 ha, medium 10-50 ha, and large >50 ha. Small and medium fragments were separated into two connectivity categories based on presence/absence of connectivity to a large forest fragment via a corridor. Corridors varied from 25-100 m in width and 37-1,071 m in length. Using pitfall traps, the study identified 21 species, terrestrial rodents the most commonly trapped species. The study found that diversity was not influenced by forest structure, but that it did influence abundance (total and individual of some species). Accounting for forest structure, the study showed that total abundance, species richness, and alpha diversity were significantly higher in connected forest fragments.

In the Amazon Basin, de Lima and Gascon (1999) investigated small mammal use of four peninsular shaped linear remnant forests that were connected to a large tract of continuous forest. The 140-190 m wide corridors extended an average of 2,225 m into a matrix that was cleared for pasture 15-19 year prior. The corridors were surrounded by secondary regrowth forest at the time of sampling. Live trapping was used to sample five transects in each corridor and adjoining forest. Fourteen species of small mammal were recorded. The study found no significant different in species richness or abundance (of the most common species) between continuous forest and corridors, as well as no distinguishable difference between small mammal communities. Breeding (presence of juveniles) and movement (through mark-recapture) were detected in the corridor and adjoining forest. The authors note matrix tolerance of a number of species in the study.

In the Atherton Tablelands of Queensland, Australia Horskins et al. (2006) used an ecological and genetic approach to assess connectivity of populations of two species of rat, *Melomys cervinipes and Uromys caudimaculatus*, by a 4.5 km long corridor in a matrix of pasture lands. They compared the genetic differentiation between within each species in the corridor and its two connected patches of forest, as well as in isolated fragments and nearby continuous forest. They established that species composition and physical structure of the corridor were comparable to that of the connected fragments and that both species occurred and were breeding along the length of the corridor. In contrast to results of similar studies, they found the same significant level of genetic differentiation in the two forest patches connected by the

corridor as were found between the isolated forest patches. The authors emphasize that species use of a corridor does not necessarily imply genetic exchange in the patches connected by the corridor.

In the Brazilian Atlantic Forest, Rocha et al. (2011) compared the composition and structure of small mammals between a single 4 m wide vegetation corridor, its two connected forest fragments (26 and 48 ha), and the adjacent coffee plantation matrix. Live traps were placed on the ground and in the vegetation 1-2 m off the ground along 14 transects (5 in corridors, 5 in the matrix, 2 in each fragment). Study results showed the corridor having the highest species richness (detecting all 15 sp.), followed by fragments (10 sp.) and the coffee matrix (6 sp.). Abundance was most similar between the fragments and corridor and significant habitat preferences were identified for six species.

Also in Brazil's Atlantic Forest, Metzger et al. (2009) tested the relationship of time-lag responses of small mammals (and other taxa) to fragment area and connectivity. Intensively fragmented, the landscape consisted of a mosaic of agricultural fields, urban areas, forest plantations, and secondary forest at various stages of regeneration. The authors sampled 21 secondary forest fragments (>15-20 years old) of varying size (>50 ha, 10-48 ha, and <5 ha) and degrees of connectivity (direct connectivity via a corridor and proximity of 20-40 m to large fragment. For comparison, they also calculated area and connectivity over three time periods (from the years 1962, 1981 and 2000). The study recorded 19 species of small mammal that they separated into two groups for analysis: forest dependent (13) and non-forest dependent (6). Regression models found that past landscape structures and dynamics had a weak influence on small mammal richness or abundance. Habitat area and the presence of corridors best explained forest small mammal species richness and abundance, with the presence of a large forest fragment 20 m away also influencing abundance. Richness and abundance of non-forest small mammals were best explained by gap crossing measures, which fits with the ability of these species to use the matrix.

In the same study where lemurs were surveyed in the southeastern escarpment of Madagascar (described in the large mammal section), a 95-km long forest corridor connecting two large national parks was studied for the functionality of the corridor

for small mammals (Ramiadantsoa et al. 2015). This corridor aligns with Category 1: Landscape linkages between reserves or large natural areas. Fifteen sites (eight in the corridor) were surveyed using standard traps and pitfall traps. The study identified 28 species and found that species richness was slightly higher in the national parks than in the corridor, with one national park more species rich than the other. The majority of species were found to have continuous distributions across the study area (corridor and national parks). The corridor and each national park had at least one species that was unique to it, with the parks sharing an additional species not present in the corridor.

Table 2.5 Summary of results from each small mammal study included in the literature review. Results are given for each commonly known corridor design component.

First author & Year	Country	Species	Width/Length of corridors sampled	Species specific response	Ability to use matrix matters	Habitat quality in corridor matters	Wider corridor > response variable*	Greater level corridor connectivity > response variable*	Core habitat > response variable than corridors*	Distance into corridor affects use	Anthropogenic factors influence use
Pardini 2005	Brazil	21 spp.	Width: 25-100 m; Length: 37 - 1,071 m	Yes	Yes, discussed, but not sampled	NA	NA	Yes	NA	NA	NA, indirectly through forest structure (logging)
de Lima 1999	Brazil	14 spp.	Width: 140-190 m; Length: 700 - 1,600 m	No	Discussed, but not tested	NA	NA	NA, only connected corridors sampled	No	NA	NA
Horskins 2006	Australia	2 rat spp.	Width: c.50 - 300 m; Length: <4.5 km	Yes	Yes, neither species present in matrix	Yes, sampled to control for difference	NA	NA	No difference in habitat use	NA, but detected at all sites in the corridor	NA
Rocha 2011	Brazil	15 spp.	Width: 4 m; Length: 3.2 km	Yes	No, species not present in matrix identified in corridor and fragments	NA	NA	NA	No	NA	NA

First author & Year	Country	Species	Width/Length of corridors sampled	Species specific response	Ability to use matrix matters	Habitat quality in corridor matters	Wider corridor > response variable*	Greater level corridor connectivity > response variable*	Core habitat > response variable than corridors*	Distance into corridor affects use	Anthropogenic factors influence use
Metzger 2009	Brazil	19 sp. (13 forest, 6 non-forest)	≤100 m wide; length not stated	Yes	Yes, discussed and species grouped initially accordingly: forest/non-forest	NA, controlled for initial site selection	NA	Yes	NA	NA	NA
Ramiadantsoa 2015	Madagascar	28 spp.	Width: 2-50 km wide; Length: 95 km	NA	NA	Yes, not tested for small mammals alone but discussed	NA	NA	Yes, species richness slightly lower in corridor. Parks more unique species.	NA	NA

*Species richness, occupancy, abundance, activity level, etc.; NA = Not addressed in the study

Summary of small mammal studies

Five of the six small mammal studies took place in fragmented agricultural and pasture landscapes, most closely resembling Category 5: local networks of linear remnants. These corridors varied from 4 to approximately 300m wide and from 37m – 4.5 km long, though none of the studies measured the effect of corridor width or length on small mammals. The other study took place in a 95 km long, 2 – 50 km wide corridor between two national parks in Madagascar – best categorized as landscape linkage (Category 1).

Only one study focused on genetic exchange, while the other five studies were community studies comparing demographic variables between treatments (i.e., fragments with and without corridors; or comparing sample sites within corridors to that of fragments, the matrix and forest patches). Four of the six studies found species specific responses to corridors. De Lima and Gascon (1999) did not find a difference in species responses, which may be a result of secondary forest growth surrounding the corridors at the time of sampling. The matrix was not sampled in this study, but if the adjoining secondary forest in the matrix was used as habitat, small mammals may have perceived the landscape as one large expanse of habitat. The Madagascar study (Ramiadantsoa et al. 2015) identified the presence of unique species in the corridor and national parks, but given the large scale of the corridor, the single corridor sample (n=1) and very slight differences in species richness, it was not clear if the lower species richness in the corridor and the presence of unique species in the corridor and national parks, was a result of corridor preference and avoidance by species or natural species distributions in the landscape.

Only two studies explicitly tested use of the matrix (Horskins et al. 2006, Rocha et al. 2011), while a third separated forest and non-forest species, presumably based on prior knowledge of the species use of the matrix (Metzger et al. 2009). Two studies acknowledged matrix permeability as a factor, but did not sample the matrix, and one did not address it for this taxonomic group.

Two studies controlled for differences in habitat in their site selection and one was confirmed through data collection on habitat variables. The other studies did not

address variability in habitat quality in the forest corridors. Therefore, none of the studies tested the importance of habitat quality in corridors for small mammals.

Two studies tested the effect of connectivity by comparing fragments with and without corridors. Both studies found that fragments connected by corridors had higher species richness and abundance (in one study only for forest-dependent species).

None of the studies tested anthropogenic influences on the efficacy of corridors for small mammals. Not surprisingly, nodes, alternate pathways and greater ecosystem connectivity (as described in Table 2.1) were not addressed in these studies.

Conclusion

Since the 1990s, studies on species and taxa-specific use of corridors in fragmented landscapes have flourished. With progressively rigorous study designs and advancement in genetic and remote sensing technology, there is an increasingly impressive body of literature identifying environmental and anthropogenic variables that influence corridor use by various taxa. Though the vast majority of corridor research has been undertaken in temperate regions, tropical studies are numerous. In this chapter I have identified study design trends in peer-reviewed, published tropical forest corridor studies and summarized the findings for mammals. I believe this is only a fraction of the data available, with much information available in gray literature and the field notebooks and laptops of biologist and conservationists working in tropical countries. Still, some clear patterns have emerged.

Although landscape scale corridors are a popular conservation strategy in tropical countries, the vast majority of scientific literature on the ability of forest corridors “to assist the movements of animals” and/or “maintain the continuity of species populations and ecological processes” (Bennett 2003), are undertaken at a much smaller scale, and are not focused on maintaining the breadth of ecological processes captured in extensive forest landscapes. Tropical corridor research is largely undertaken in fragmented agriculture and pasture-dominated landscapes, and predominantly in Latin America, though studies in forestry plantation are also present.

Larger scale, landscape studies are oriented towards connectivity for large mammals of conservation concern.

The studies reviewed revealed a strong trend toward observational research using demographic variables to compare corridor use to forest patches, continuous forest and the matrix, and infer connectivity through corridor use. The mammal studies largely supported corridor design recommendations from temperate corridor studies, showing: species-specific responses to corridors; direct connectivity via corridors increases species richness and abundance in forest fragments; habitat quality in the corridor are important to functionality; and anthropogenic disturbances (hunting, logging, transport corridors, settlements, and mining) have a negative impact on corridor use.

Corridor width was only tested in five studies, with most studies finding that wider corridors increase species richness, noting an increase in habitat quality in wider corridors. Collectively these studies advocate that wider riparian buffers are better suited to serve as movement corridors and habitat, and that a minimum buffer width of 100m (50 m either side of a river) is necessary to support forest dependent species, but that up to 400m in width is necessary to retain the same species richness of forest dependent species as connected core areas (Laurance and Laurance 1999, Lees and Peres 2008, Nasi et al. 2008, Yaap et al. 2016, Zimbres et al. 2017). Although not widely studied, it is expected that tropical corridors aiming to maintain species richness in the landscape will need to be wider than those in temperate region due to a higher number of forest interior specialists in tropical regions and the higher level of vulnerability of tropical forests to edge effects (de Lima and Gascon 1999, Thier and Wesenberg 2016).

The effect of corridor length was also infrequently studied, with species specific responses in the four studies that did address this variable. Alternate pathways and habitat nodes along corridors were not addressed in any of the studies, likely reflecting the lack of such features in tropical landscapes.

So, what next? It has been said that there are no universal rules to corridors, reflecting the nature of the field of ecology (Chetkiewicz et al. 2006). And as Bennett (2003)

states, it is “neither possible nor desirable to provide specific uniform guidelines” for landscape linkages. Both are correct, but the problem is that the vast majority of people making decisions on landscape structure and connectivity in tropical countries are unlikely to engage in heavy bodies of literature or scientific studies to guide decisions on how they will fragment their landscape. As scientists, do we simply continue to accumulate an increasingly impressive species- and location-specific body of information on forest corridors, refining the known list of biological issues that influence corridor function and effectiveness as we go?

In tropical forest regions of the world that face of rapid deforestation, strong guidelines for agricultural and forestry landscapes based on evidence could secure these areas to enable greater sustainability. Guidelines could be produced on a regional basis, based on individual or key groups of threatened species with context and matrix specific scenarios. The conclusions arrived at by the studies in this review that address riparian buffer width and habitat quality are already a strong indication that current requirements in tropical countries are insufficient to maintain forest quality in the corridors and habitat for forest dependent species that use them. Introduction of guidelines to industry and government that integrate these findings alone, and placed in the hands of locally active social and environmental NGOs, will at least allow for the possibility of informed decisions on biodiversity conservation, corridors and landscape connectivity in the world’s quickly disappearing tropical forest landscapes.

Chapter 3 Maximizing automatic-camera detection of rainforest mammals with scent lures

This chapter is based upon a paper in preparation:

Yaap, Betsy [a] and William F. Laurance[a]. In prep. Maximizing automatic-camera detection of rainforest mammals with scent lures. Journal to be determined.

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Statement of contribution of others:

Laurance provided guidance on study design and analysis and edited multiple drafts of the manuscript.

Abstract

Rapid biological assessments are vital for biodiversity conservation, with camera traps being among the most effective tools for surveying larger mammals (>1 kg). Scent lures are attractive to at least some species, but their effects in tropical rainforests and potential deterrent effects on some species are unknown. Here I evaluate the effect of a common scent lure on species richness, composition and detection frequency of larger (>1 kg) mammals in rainforest in Riau Province, Sumatra, Indonesia. Using a paired study design, twenty-seven sets of camera traps were placed in remnant riparian-forest strips within a large industrial *Acacia* plantation and nearby rainforest reserves. For each pair, cameras were placed on animal trails, spaced approximately 50 m apart, with one randomly selected camera baited with a commercially available scent lure (Carman's Magna-Glan Lure) and the other unbaited. Mammal species richness was compared between baited and unbaited traps using paired t-tests. Species composition, detection frequency and time to first detection were also contrasted. Species richness estimates increased significantly with the use of lure, seemingly without altering species composition. Time to first detection varied among species, with threatened mammal species being detected more quickly with lure. The largest increase in species richness occurred in the second week of surveys for both baited and unbaited cameras. In rapid assessments aimed at detecting presence of rainforest mammals, I recommend two-week camera-trapping sessions using a scent lure. The paired design provides a powerful and direct test of attractant efficacy, and clearly demonstrates that baited camera traps perform better than unbaited traps for detecting mammals in this rainforest environment, apparently without introducing significant sampling bias.

Introduction

Wildlife can be very difficult to detect and study in dense tropical forests. Current techniques for detecting larger mammals include track and sign surveys, direct observations, camera trapping and interviews with local communities and hunters. Camera trapping is an increasingly popular method, with numerous studies showing camera traps to be effective for surveying larger (>1 kg) mammals, especially rare,

elusive or nocturnal species (some examples include Silveira, Jacomo and Diniz, 2003; Kelly, 2008; Tobler et al., 2008; Espartosa, Pinotti and Pardini, 2011; O'Connell, Nichols and Karanth, 2011). Automatic cameras are particularly useful in dense tropical forests where track surveys and direct observations are difficult to conduct.

Attractants such as scent lures or edible baits have often been used to improve detection of larger mammals in temperate regions. However, few studies have assessed attractants in tropical rainforests, where dense vegetation, low wind speeds and high humidity might affect scent dispersal. A study in Brazil compared locally available scent lures with food bait (bananas, corn and salt) for attracting domestic dogs and cats, finding the scent lure ineffective but the food bait effective (Espartosa et al., 2011). Also in Brazil, Michalski and Peres (2007) baited camera traps with a commercially available wild cat scent, but had no controls (camera traps without bait) for comparison.

A key concern is whether a particular bait or lure may attract some species and deter others, thereby creating sampling biases that could confound comparisons among different studies. To my knowledge, a rigorous, paired comparison—with and without an attractant—to test attractant efficacy for tropical forest mammals has not yet been conducted. Here I compare detections of larger (>1 kg) mammals between paired cameras with and without Magna Glan scent lure in Sumatra, Indonesia. This bait has been recommended for mammal surveys in this region (Giman et al., 2007), and my goal was to evaluate its effect on estimates of species richness, composition and detection frequency of rainforest mammals.

Methods

Study area

This study was conducted in lowland tropical rainforest embedded within and abutting an *Acacia* mangium wood fiber plantation in Riau, Sumatra, Indonesia (0°18'-0°24 S, 101°52'-102°0'E) (Figure 3.1). The plantation borders Tesso Nilo National Park (TNNP), which is known to harbor the complete array of medium- and large-sized mammals native to lowland rainforest (excluding flooded forests) in the region. Located just

south of the equator, the site has a mean annual rainfall of 2600 mm with a drier period in July (averaging ~120 mm) and the wettest period in November (averaging ~300 mm). Temperature is quite consistent throughout the year, with a mean high of 31°C and a mean low of 23°C.

By law, the *Acacia* plantation maintains a network of riparian forests (50-100 m wide) buffering rivers that are at least 5 m in width, as well as conservation set-aside areas (Nasi et al., 2008). Unplantable, seasonally flooded forests and patches of regenerating forest add to the complexity of the plantation landscape. A number of the riparian forest buffers connect directly with remnant forest in TNNP, whereas others are effectively isolated within the plantation and disappear at the southern and eastern borders of the plantation where the landscape shifts to oil palm and rubber plantations (Figure 3.1). To the west, the plantation is bordered by another *Acacia* plantation. The linear remnant forests in this study area align with linkages in forest conservation and management (Category 3 in Chapter 2) as described by Bennett (2003). These linkages are typified by production forest landscapes where remnant natural forest strips are embedded in a patchy matrix of production forest at different stages of regrowth.

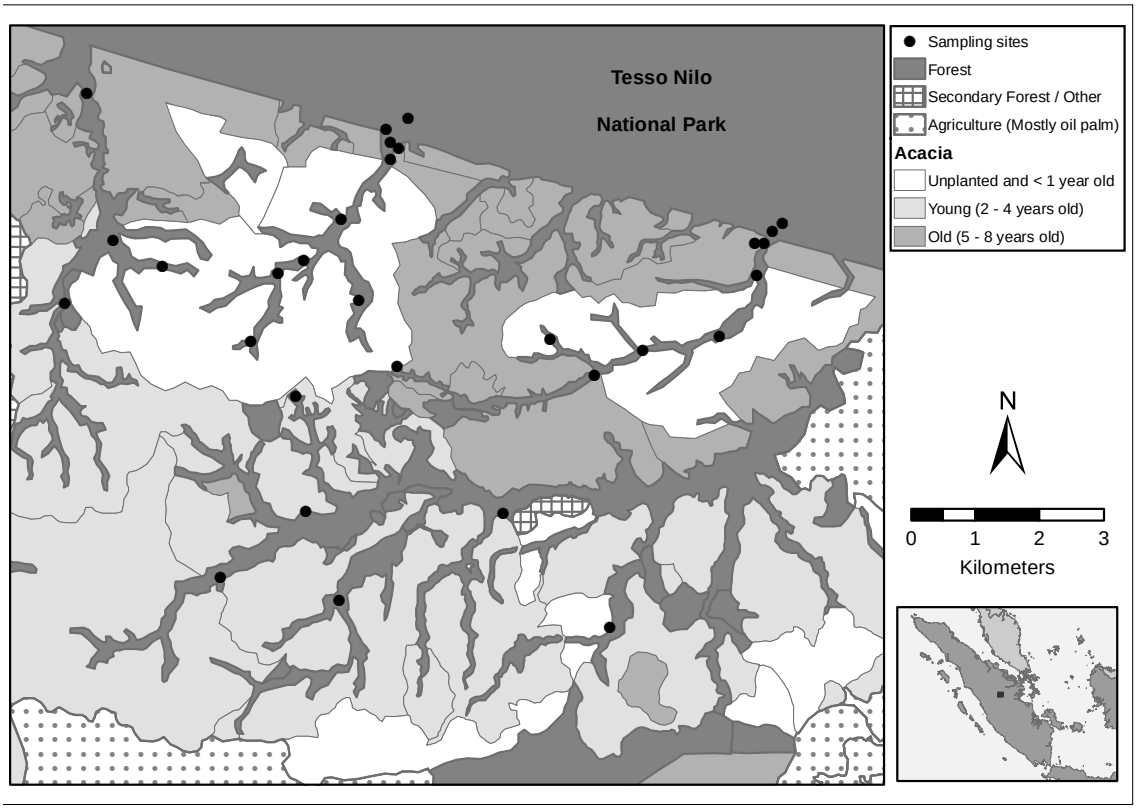

Figure 3.1 Study area and sample sites located in an *Acacia mangium* plantation in Riau, Sumatra, Indonesia. Black circles denote each pair of camera traps spaced approximately 50 m apart.

Camera-trap surveys

Surveys were conducted between July 2011 and January 2012, using 20 Reconyx Hyperfire HC500 infrared camera traps. Cameras were used for three survey periods, for ~80 nights from July-September, for ~50 nights from October-November, and for ~60 nights from November-January. In total I had 3,337 trap days (1,739 trap days for cameras with scent lure, and 1,598 trap days for unbaited cameras). Cameras were set in pairs, but placed ~50 m apart. For each pair, one of the two cameras was randomly selected for treatment with Magna Glan, which was placed on a stick ~2m in front of the camera. All cameras were set along animal trails.

Cameras were locked to trees ~40 cm from the ground using cable locks. A metal protective casing was used to prevent theft and silica gel packets were placed inside the camera casing to absorb moisture. Cameras were programmed to take three photos (one per second) at each detection. Some detection events comprised

hundreds of photos of an individual animal (e.g., a sun bear wallowing in the lure for several minutes).

Data analysis

All images were viewed and independent detections recorded. Consecutive detections of the same species were considered independent if there was >30 minutes between detections. Only mammals weighing >1 kg were included in the analyses. Lesser (*Tragulus kanchil*) and greater mouse-deer (*T. napu*) detections were combined, as these species could not be consistently discriminated.

Paired t-tests were used to compare species richness, detection frequency and the time to first detection (TFD) between cameras with and without scent lure. Data (the difference between the values for each camera pair) were log-transformed if non-normally distributed. A sign test was used for paired observations when the normality assumption of the paired t-test was not met. Species-discovery curves were also used to compare species richness between surveys. Species composition was explored by comparing the number of cameras with and without lure for each species was detected at least once. Mean TFD values for each species were also compared. Finally, the conservation status of species was compared using Red List data from the International Union for Conservation of Nature (iucnredlist.org), to determine whether cameras with lure were detecting threatened species (likely to be the target of conservation programs) more frequently than were unbaited cameras.

Results

Species composition and detection frequency

Nineteen mammal species were detected over the course of the three surveys (Table 3.1). This constitutes about half of the terrestrial and semi-terrestrial species I considered likely to be present in the study area. Species composition was broadly similar between baited and unbaited cameras, with just a few rare species (≤3 detections) not being detected via both methods (Table 3.1).

The pig-tailed macaque (*Macaca nemestrina*), sun bear (*Helarctos malayanus*), red barking deer (*Muntiacus muntjak*) and Malay tapir (*Tapirus indicus*) were the most

frequently detected species, both in overall detections and the number of cameras that detected them (Table 3.1). Carnivores and the Sunda pangolin (*Manis javanica*) were among the least frequently detected species. Most species potentially present but not detected are rare, elusive, and/or aquatic.

Although Magna Glan scent lure was designed to target North American carnivores and omnivores (bobcat, fox, raccoon), in Sumatra it appeared most attractive to omnivores and herbivores, with the responses of carnivores being more variable (Table 3.1). Several cat species were detected more often at unbaited cameras, except for the marbled cat (*Pardofelis marmorata*), which was recorded more frequently at baited cameras. With low detection frequencies overall, it is difficult to attribute detections of most cats, civets, the yellow-throated marten (*Martes flavigula*) and pangolin to the presence or absence of scent lure. The Malay civet (*Viverra tangalunga*) is an exception, showing a strong attraction to the scent lure (4 versus 17 detections). The short-tailed mongoose also was detected more frequently at baited cameras (1 versus 5 detections).

Surprisingly, I had few detections of the leopard cat (*Prionailurus bengalensis*), a species known to frequent *Acacia* plantations and commonly captured by camera traps. Asian elephants were detected in the survey areas via direct and indirect observations, but were not recorded by the cameras. The Asiatic dhole (*Cuon alpinus*), frequently detected in a nearby region of Sumatra (Maddox et al. 2007), was not detected, nor were two of the six felids present in Sumatra, the Asiatic golden cat (*Pardofelis temminckii*) and flat-headed cat (*Prionailurus planiceps*).

Overall, baited cameras had significantly more mammal detections than did unbaited cameras (paired $t = 2.32$, d.f. = 26, $P = 0.03$). This was largely because of frequent visits to baited cameras by sun bears, Malay porcupines, mouse deer, long-tailed porcupines, and Malay civets. Fourteen of the 19 species I detected were recorded more frequently at baited cameras (Table 3.1). However, among the seven 'commonest' species (detected at ≥17 of the paired sites; Table 3.1), detection frequency differed significantly only for the Malay civet (sign test, $P < 0.001$).

Table 3.1 Large mammal species detected in an *Acacia mangium* plantation in Riau, Sumatra, including their IUCN Red List status, diet, and the proportion of baited and non-baited cameras that detected each species at least once.

				Proportion of cameras detecting the species (no. of detections)	
Scientific name	**Common name**	**IUCN**	**Diet**	**No lure**	**Lure**
Carnivora					
Neofelis diardi	Clouded leopard	VU	C	0.04 (1)	0.00 (0)
Prionailurus bengalensis	Leopard cat	LC	C	0.07 (3)	0.00 (0)
Panthera tigris sumatrae	Sumatran tiger	CR	C	0.07 (2)	0.03 (1)
Pardofelis marmorata	Marbled cat	NT	C	0.07 (2)	0.17 (7)
Paradoxurus hermaphroditus	Common palm civet	LC	O	0.07 (2)	0.07 (2)
Viverra tangalunga	Malay civet*	LC	O	0.15 (8)	0.60 (41)
Arctictis binturong	Binturong	VU	O	0.00 (0)	0.03 (1)
Herpestes brachyurus	Short-tailed mongoose	NT	C	0.04 (1)	0.17 (6)
Martes flavigula	Yellow-throated marten	LC	O	0.00 (0)	0.07 (2)
Helarctos malayanus	Sun bear*	VU	O	0.63 (48)	0.73 (95)
Artiodactyla					
Sus scrofa	Eurasian wild pig*	LC	O	0.59 (38)	0.60 (32)
Tragulus spp.	Mouse deer	LC	H	0.26 (37)	0.30 (62)
Rusa unicolor	Sambar deer	VU	H	0.07 (2)	0.17 (6)
Muntiacus muntjak	Red barking deer*	LC	H	0.48 (56)	0.63 (50)
Perissodactyla					
Tapirus indicus	Malay tapir*	EN	H	0.52 (40)	0.57 (58)
Rodentia					
Hystrix brachyura	Malay porcupine*	LC	O	0.41 (34)	0.53 (51)
Trichys fasciculata	Long-tailed porcupine	LC	O	0.04 (1)	0.10 (20)
Primates					
Macaca nemestrina	Pig-tailed macaque*	VU	H	0.89 (90)	0.90 (95)
Pholidota					
Manis javanica	Sunda pangolin	CR	I	0.04 (1)	0.00 (0)
Total				(366)	(529)

C = carnivore, O = omnivore, H = herbivore, I = insectivore; No lure: n=27; lure n=30

* Detection frequency tested using paired t-test (refer to text)

Species richness

Species richness was compared using six weeks of data from 27 paired cameras (2,086 trap days). If a camera failed, data from its paired camera were also removed. Species richness was significantly higher (paired t = 3.63, d.f. = 26, P = 0.001) at cameras baited with scent lure (mean ± SD = 5.33 ± 1.99 species) than at unbaited traps (3.85 ± 1.96 species).

The effects of baiting appeared to persist for a considerable period. When examined cumulatively (progressively adding data from each week), species richness was significantly elevated in baited traps from week 2 onward (Table 3.2). The effect increased over the first four weeks, then leveled off in weeks 5 and 6. When each week was examined individually, however, species richness did not differ significantly between baited and unbaited cameras.

Species-accumulation curves were used to determine the number of trap days required to reach maximum species richness for each survey, with and without lure (Figure 3.2). In all three surveys, the first and second weeks of sampling had the greatest increase in species richness, for both baited and unbaited cameras. Baited cameras had higher species richness in two of the three surveys.

Globally threatened species (Vulnerable, Endangered, or Critically Endangered on the IUCN Red List; Table 3.1) were detected slightly more rapidly at baited cameras in two of the three surveys. However, the number of threatened species detected after six weeks was comparable between baited and unbaited cameras (Table 3.3).

Table 3.2 Paired t-test results of cumulative species richness of cameras with and without lure as sample period (number of weeks cameras are deployed) increases.

				Mean (SD)	
Week	t	d.f.	*P*	No Lure	Lure
1	2.06	26	0.059	1.4 (±1.4)	2.1 (±1.6)
1-2	2.06	26	0.029	2.4 (±1.8)	3.2 (±1.4)
1-3	2.06	25	0.010	3 (±1.9)	4.2 (±1.5)
1-4	2.06	24	0.002	3.2 (±1.8)	4.6 (±1.7)
1-5	2.08	21	0.005	3.7 (±1.9)	5 (±2.7)
1-6	2.08	21	0.003	4.2 (±1.9)	5.9 (±1.7)

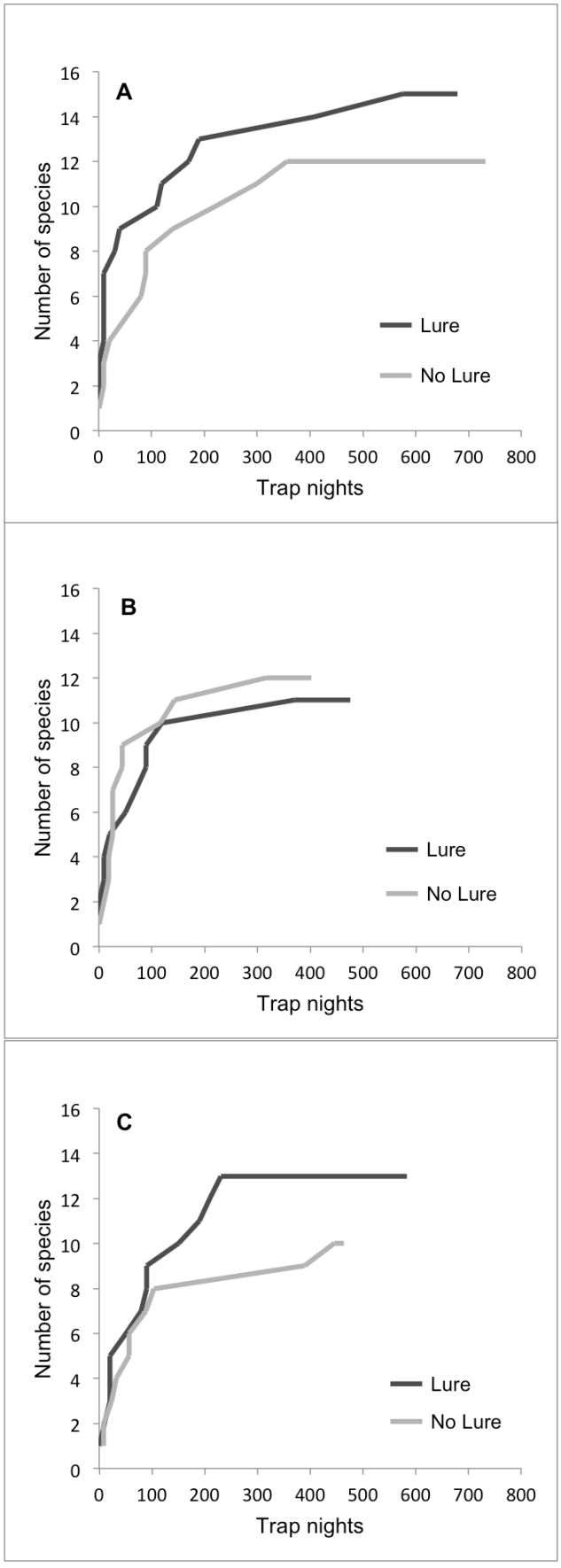

Figure 3.2 Species discovery curves for large mammals detected during three camera trapping survey periods in Riau, Sumatra.

Table 3.3 Large mammal species accumulation shown in species richness by survey week, with cumulative count of International Union for the Conservation of Nature (International Union for Conservation of Nature [IUCN] 2016) Red List threatened species (i.e., Vulnerable, Endangered or Critically Endangered).

	Species richness (No. of threatened species)					
	Survey A		Survey B		Survey C	
Week	No lure	Lure	No lure	Lure	No lure	Lure
1	5 (2)	9 (4)	9 (3)	7 (3)	6 (3)	6 (3)
2	9 (4)	11 (5)	10 (4)	10 (4)	8 (4)	9 (5)
3	10 (4)	12 (5)	11 (4)	10 (4)	8 (4)	12 (5)
4	10 (4)	13 (6)	11 (4)	10 (4)	8 (4)	13 (5)
5	11 (5)	13 (6)	11 (4)	10 (4)	8 (4)	13 (5)
6	12 (6)	13 (6)	12 (5)	11 (4)	8 (4)	13 (5)

Time to first detection

For the eight most frequently detected species, four (Malay civet, sun bear, Malay tapir, and Malay porcupine) were detected sooner on average with lure (Figure 3.3). Time to first detection (TFD) was similar between baited and unbaited cameras for three species (pig-tailed macaque, red barking deer, and Eurasian wild pig), whereas the mouse deer had a longer TFD at baited cameras.

More baited cameras detected each species than non-baited cameras for all of the eight most frequently detected species, except for the mouse deer, which was detected on an equivalent number of baited and non-baited cameras. This suggests that the lure does not have a deterrent effect on any of these eight species. Photo evidence shows a clear interest in scent baits for all of these species (Figure 3.4). The remaining species were detected too infrequently to assess the influence of the lure (Table 3.1).

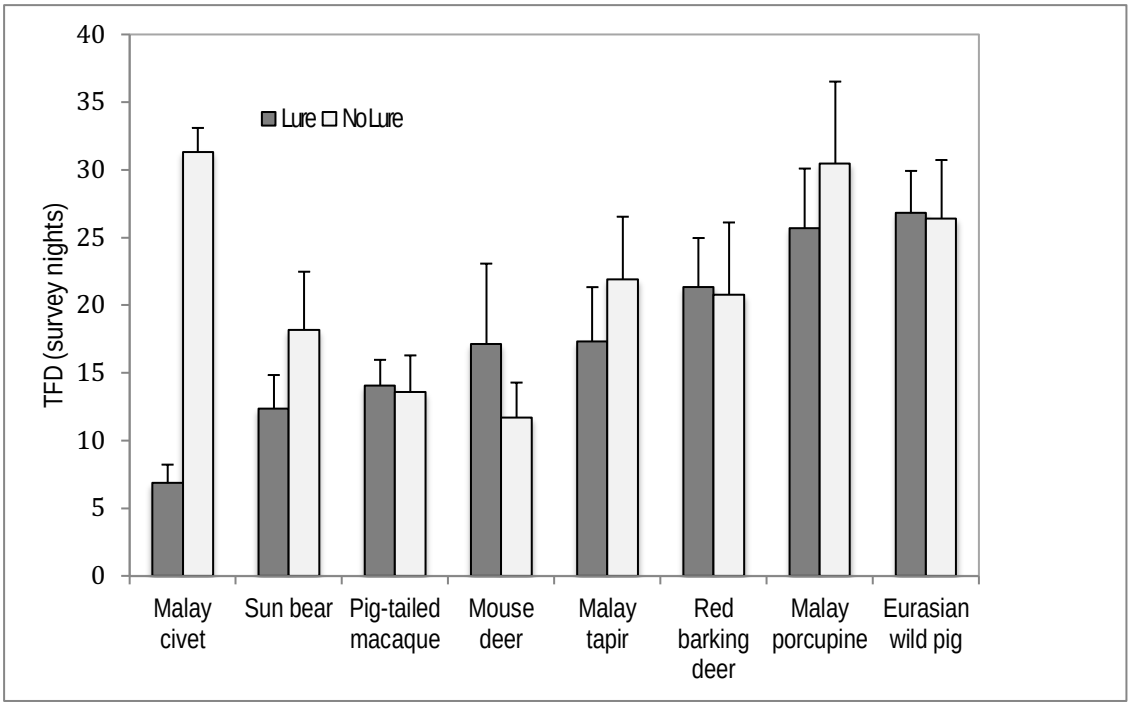

Figure 3.3 Mean time to first detection (TFD) for the seven most frequently detected species, subdivided by cameras with and without lure, at the study site in Riau, Sumatra.

Figure 3.4 Camera trap photos of large mammals responding to scent lure in an *Acacia mangium* plantation in Riau, Sumatra. Clockwise from the top left: A male sun bear (*Helarctos malayanus*) - this species was photographed rolling in the lure, and here, rubbing the stick and lure around his head and neck; A male red barking deer (*Muntiacus* muntjak); Malay civet (*Vivierra tangalunga*) - this species showed a strong attraction to the scent lure; Two Malay tapirs (*Tapirus indicus*); A pig-tailed macaque (*Macaca nemestrina*); A Malay porcupine (*Hystrix brachyura*).

Discussion

Using camera traps, I found that a commercial scent lure (Magna Glan) increased the overall detections and estimates of species richness of larger forest mammals in Sumatra, Indonesia. Detections of the Malay civet were dramatically increased by the lure, with most of the other 18 species I recorded also showing somewhat higher detection frequencies at baited cameras. The increased effectiveness of lures was especially pronounced for threatened species. No deterrent effect of the bait was apparent for the species I encountered.

Improved species detection is particularly important for rapid biodiversity assessments, where the focus is usually on creating a species inventory and identifying areas of high conservation value. These rapid assessments have become common practice in development landscapes. In Indonesia, for example, companies attempting to meet third-party certification criteria (e.g., Forestry Stewardship Council, Roundtable on Sustainable Palm Oil) usually outsource biodiversity surveys. Time and resource constraints often demand that biodiversity assessments be completed in two weeks or less.

Although some rare or elusive species will only be detected with lengthier surveys of over 1,000 trap days (Tobler et al., 2008), the use of camera traps and scent lure can improve the number of species detected and provide tangible evidence of threatened species. Based on my results, I recommend that rapid biodiversity assessments sample the area of interest for as many days and with many cameras as is feasible, rotating cameras to new sites every two weeks. I recommend Magna Glan scent lure to maximize detection of omnivores and herbivores, at least in Southeast Asia. Further trials are needed to identify specific baits and lures that may increase detections of carnivores.

I also used camera traps with Magna Glan in Costa Rica (Chapter 5) and found that many mammals there also appeared to be strongly attracted to the bait, often showing an active interest in baited sticks. This can be an advantage for studying species such as jaguars, in which individuals can be identified by their unique rosette patterns. On multiple occasions my cameras photographed jaguars in a series of

photos while interacting with a baited stick. Maneuvering around the baited stick allowed for photos of both flanks to be recorded in one detection event with one camera. Cameras are often set in pairs to collect such data and identify individuals by their unique patterns, whereby this was achieved with a single camera and bait. Use of bait could therefore allow for greater efficiency of camera resources while still allowing for individual identification.

Chapter 4 Large mammal use of riparian forest corridors in Sumatra, Indonesia

This chapter is based upon a paper accepted to Tropical Conservation Science (Nov 2016), with minimal format and content edits.

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Statement of contribution of others:

Yaap was the lead author and lead researcher (study design, field data collection, data analysis and interpretation). Magrach, Clements and McClure provided guidance on statistical analysis and interpretation and input on manuscript drafts. Paoli provided input on study design and feedback on results and manuscript drafts. Laurance provided guidance on study design and analysis and reviewed and edited the manuscript.

Abstract

Riparian forests are often the last remaining areas of natural vegetation in agricultural and plantation forestry landscapes. Covering millions of hectares of land in Indonesia, industrial pulpwood plantations have rapidly replaced native forests. This study aimed to better understand the conservation importance of linear remnants of riparian forest by examining their use by larger (>1 kg) mammal species. The study site was located within an extensive *Acacia* (*Acacia mangium)* plantation adjoining Tesso Nilo National Park in Sumatra, Indonesia. Camera traps were used to detect mammals at 57 sites to assess the effects of corridor-design and land cover covariates and species behavioral traits on mammal habitat use of four linear riparian forests. I recorded 17 species (including one IUCN Critically Endangered, two Endangered and four Vulnerable) in riparian forests inside the plantation, including the Sumatran tiger (*Panthera tigris* sumatrae), Malay tapir (*Tapirus indicus*) and sun bear (*Helarctos malayanus*). Some threatened species were detected in the park buffer zone. Species varied in their responses to riparian forests, but distance to the national park, remnant width, and percent forest cover around the camera site were common predictors of remnant use. Many mammal species used riparian forests regardless of whether they were surrounded by intact *Acacia* forests or recently cleared land. The results indicate that linear remnant riparian forests ≤ 200 m in width can facilitate local (< 4 km) movements of many large mammal species in Sumatra, but wider riparian remnants would likely be more effective at promoting mammal movements over longer distances.

Introduction

Production landscapes threaten tropical ecosystems in Indonesia through deforestation, inadequate governance and poor management of knock-on effects associated with development (Holmes 2002, Murdiyarso et al. 2011, Paoli et al. 2013, McCarthy and Zen 2010, Miettinen et al. 2011). Indonesia has suffered large environmental losses with the conversion of natural forests to production landscapes, especially oil palm and pulpwood plantations (Abood et al. 2015, Fitzherbert et al. 2008, Obidzinski and Dermawan 2012). Against this backdrop, conservation strategies

that incorporate production landscapes have become increasingly popular drawing attention to factors affecting their conservation value (Wilson et al. 2010, Yaap et al. 2010, e.g., Laurance et al. 2010).

Riparian forests are afforded legal protection in Indonesia (Republic of Indonesia 2011) and often constitute the last remnants of native forest in industrial production landscapes, such as wood pulp and oil palm plantations. When in close proximity to larger blocks of native forest, remnant linear strips of riparian forest can potentially serve as corridors for forest-dependent species, facilitating access to forest fragments embedded in a plantation matrix, and providing connectivity across the broader landscape (McShea et al. 2009, Nasi and Frost 2009).

Pulpwood plantations are rapidly expanding in Indonesia and have replaced extensive areas of natural forest (Abood et al. 2015, Obidzinski and Dermawan 2012). Covering millions of hectares of land - estimated at 4.9 million ha in 2010 and with a national target to triple planted areas to 14.7 million ha by 2030 (Obidzinski and Dermawan 2012) - wildlife friendly pulpwood plantations could play an important role in conserving biodiversity. These plantations (predominantly *Acacia* and *Eucalyptus* spp.) are often adjacent to protected areas and large blocks of native forest, especially in Sumatra (WWF 2006, Last Chance to Save KKI Warsi et al. 2010); . By law, industrial plantations are required to maintain a network of riparian forests of 50-100 m width on either side of rivers (Republic of Indonesia 2011), but in practice, these riparian buffers are highly variable based on company interpretations of various laws (Nasi et al. 2008) and different levels of illegal forest encroachment. Wider buffers tend to be associated with unplantable (steep gradient) and seasonally flooded forests.

Empirical studies on the use of biological corridors (including linear remnant forests) have largely focused on temperate regions (de Lima and Gascon 1999, Laurance and Laurance 1999, Lees and Peres 2008). Decades of corridor research suggest that a number of factors can influence the functionality of corridors, including ecology of the target species, corridor width and length, matrix permeability, habitat quality in the corridor, level of connectivity (i.e., presence of gaps), presence of alternate pathways and nodes (i.e., resting spots along a corridor), anthropogenic disturbances, overall ecosystem connectivity, and, importantly, political will for implementation (Beier et al.

2008, Hilty et al. 2006, Laurance 2004, Lindenmayer and Nix 1993, Bennett 2003, United States Department of Agriculture [USDA] 2004, Jain et al. 2014, Fischer et al. 2006).

Studies on connectivity through linear forest remnants have been undertaken in fragmented agricultural and pasture landscapes in the American tropics (Barlow et al. 2010, Lees and Peres 2008, Ibarra-Macias et al. 2011a), but few such studies have focused on large mammals or riparian forests, especially in tropical Asia. To date, only two studies have assessed the use of remnant forests by large mammals in Southeast Asian plantations. In Sumatra, Nasi et al. (2008) identified a need for direct connectivity of riparian remnants (with no gaps) to allow movements of primates and underscored the importance of habitat quality in the remnants. In Malaysian Borneo, McShea et al. (2009) found that forest type (secondary forest versus *Acacia* plantation) and proximity to secondary forest affected remnant occupancy for seven large mammal species.

This study aims to better understand the use of linear remnant riparian forests by large mammals in an *Acacia* (*Acacia mangium*) plantation in Sumatra, Indonesia. In addition to determining the species composition of mammals using linear remnants, I also investigate how remnant use is influenced by corridor-design covariates such as (a) remnant length and width, (b) remnant connectivity, (c) distance to a core forest habitat (Tesso Nilo National Park), as well as (d) surrounding land cover (including the presence and age of the surrounding *Acacia* plantation). I hypothesize that (1) wider and shorter remnants, (2) connected remnants, (3) sites located closer to the national park, and (4) remnant sites with more native forest or older *Acacia* plantations are more likely to be used by larger mammals. Based on my findings, I provide management recommendations to improve the function of riparian remnants as corridors in Sumatran agricultural and plantation forestry landscapes.

Methods

Study Area

This study was conducted from July 2011 – January 2012 in lowland tropical rainforest embedded within and abutting an *Acacia mangium* wood fiber plantation in Riau, Sumatra, Indonesia (0°18'-0°24'S, 101°52'-102°0'E) (Figure 1.1). The plantation borders Tesso Nilo National Park (TNNP), which is likely to harbor the complete array of medium- and large-sized mammals native to Riau's lowland rainforests (excluding flooded forests) (International Union for Conservation of Nature [IUCN] 2016, Nasi et al. 2008, ProForest 2006). Located just south of the equator, the site has a mean annual rainfall of 2600 mm with a drier period in July (averaging ~120 mm) and the wettest period in November (averaging ~300 mm). Temperature is relatively consistent throughout the year, with a mean high of 31°C and a mean low of 23°C.

At the time of survey, the plantation was dominated by *Acacia* stands of varying ages (<1 - 8 years old) and a network of riparian forests ranging from 80 – 1000 m in width. Some of the riparian forests connect directly with native forest in TNNP at the northern border of the plantation. Towards the southern and eastern borders of the plantation, riparian forests exist as islands within the *Acacia* matrix, disappearing where the landscape shifts to oil palm and rubber plantations (Figure 4.1). To the west, the plantation is contiguous with another *Acacia* plantation that is similar in layout to the plantation I surveyed. All riparian forests in the study area had breaks in forest cover where management roads (typically 15 - 20 m wide) traversed the linear remnants, though many of these roads supported vegetation themselves and were impassible to vehicles in older *Acacia* stands. Smaller areas of conservation forest set-asides, typically unplantable and seasonally flooded forests, and patches of contested land with regenerating forest, were also present in the landscape.

The *Acacia* plantation was undergoing its first harvest during the year the survey took place, leaving some riparian forests surrounded by a deforested landscape of bare soil (Figure 4.2 A) or newly planted seedlings (Figure 4.2 B and Figure 4.2 C). I refer to these as "high-contrast remnants" because they lack the *Acacia*-tree matrix that larger mammal species may use and have a sharply contrasting edge along the forest-

plantation transition. Track surveys in areas surrounding the high-contrast remnants revealed very few signs of mammal use, but these remnants were not truly isolated because they maintain connectivity to the national park and/or *Acacia* matrix at one or both ends (Figure 4.1) and some mammal species may occasionally cross these expanses of bare soil and newly planted seedlings.

As mentioned in Chapter 3, the linear remnant forests in this study area align with linkages in forest conservation and management (Category 3 in Chapter 2) as described by Bennett (2003). These linkages are typified by production forest landscapes where remnant natural forest strips are embedded in a patchy matrix of production forest at different stages of regrowth.

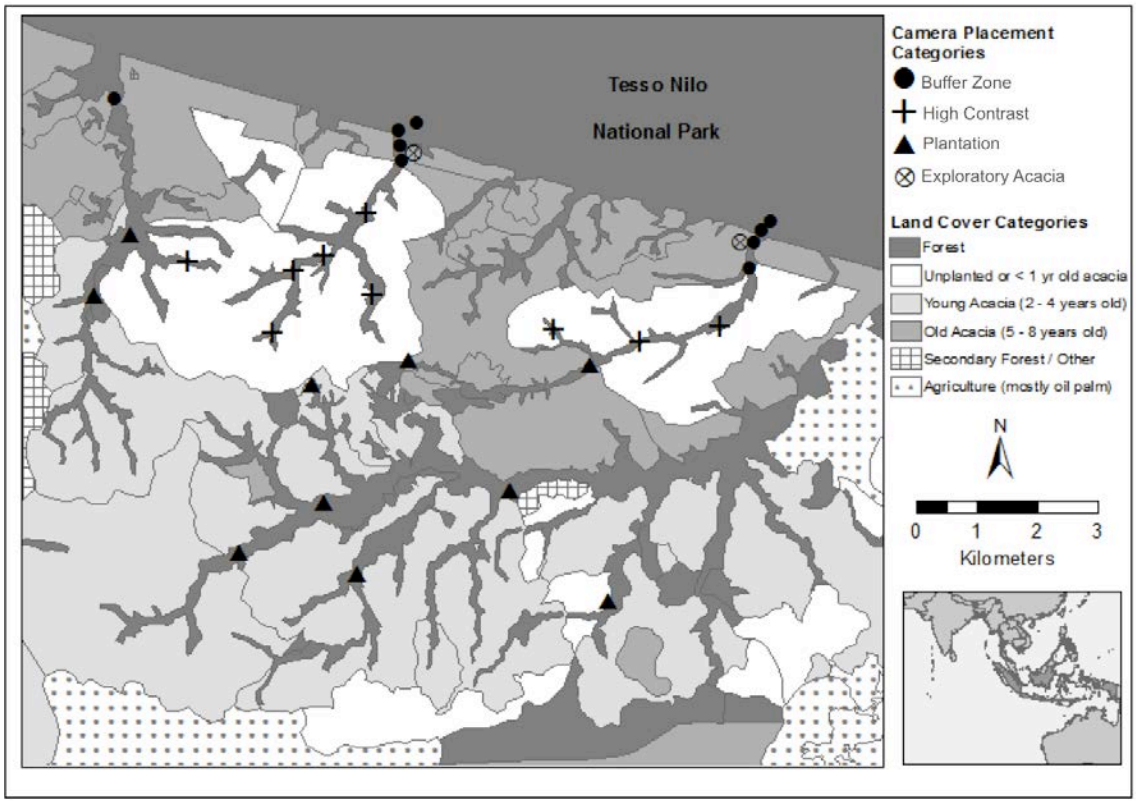

Figure 4.1 Study area located in an *Acacia mangium* plantation in Riau Province, Sumatra, Indonesia, showing camera trap sites that fall into three placement categories: (1) sites in riparian forests located in the buffer zone of Tesso Nilo National Park, (2) sites in riparian forests bordered by cleared land, also referred to as "high contrast" forest remnants, and (3) sites located in riparian forests located deep in the plantation and surrounded by acacia stands of varying ages. Additionally, two exploratory sites where cameras were placed within *Acacia mangium* stands are shown.

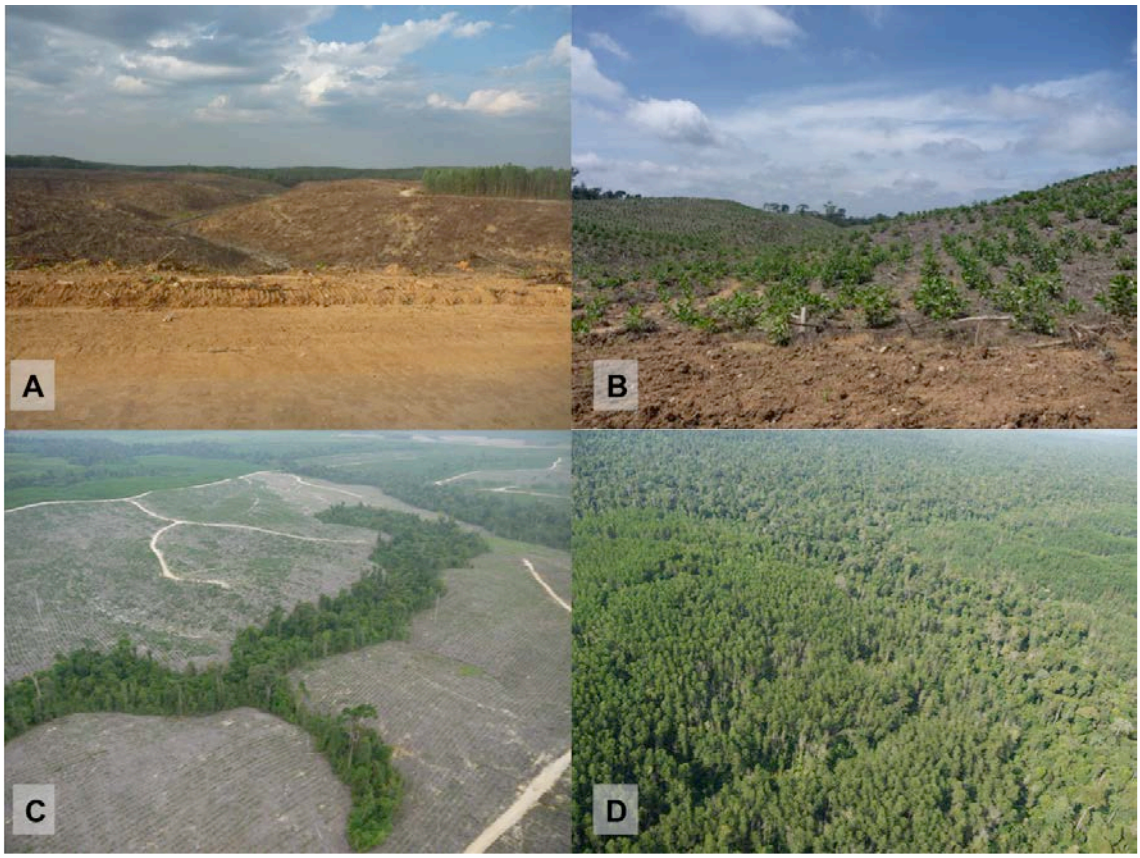

Figure 4.2 Photos of the *Acacia mangium* plantation surveyed in Riau Province, Sumatra, Indonesia, showing the barren landscape surrounding "high-contrast" remnants which includes (A) recently harvested areas, and (B) recently planted areas. Aerial photographs of the plantation showing (C) a "high contrast" remnant in newly planted *Acacia* and (D) a linear remnant embedded in an 8-year-old *Acacia* plantation (the most mature *Acacia* in the study site) at the point where it adjoins Tesso Nilo National Park.

Survey Design and Camera Trapping Protocol

I deployed 20 camera traps (Reconyx Hyperfire HC 500, Wisconsin, USA) to detect larger mammals in riparian forests near TNNP and the adjacent *Acacia* plantation (Figure 4.1). I camera-trapped 53 sites over three trapping rounds along a distance gradient in four riparian forests; three of which were directly connected to TNNP. The linear remnant forests sampled ranged from 80 – 530 m (mean = 207 m, SD = 112 m) in width, with seasonally inundated riparian areas being up to 850 m wide in one remnant. I deployed an additional four cameras in the *Acacia* matrix. Based on the study design for testing the effectiveness of bait (Chapter 3), cameras were paired and placed ~50 m apart, with one baited and one unbaited. Although deemed "paired" for

the bait study, cameras were analyzed as independent sites for this chapter, with their independence tested prior to analysis as described below. For each pair, I randomly selected one camera for treatment with scent lure (Ross Carman, Magna Glan, New Milford, PA, USA) (Chapter 3). I attached all cameras to trees, ~40 cm above ground, along animal trails. The cameras were set and left unchecked for three consecutive periods ranging from 7 to 12 weeks. I catalogued all camera images and considered consecutive detections of the same species to be 'notionally independent' if there was >30 minutes between detections. I combined lesser (*Tragulus kanchil*) and greater (*T. napu*) mousedeer detections, as these two species could not be consistently discriminated.

Corridor-design covariates

Using ArcGIS (version 10; ESRI, Inc., Redlands, CA, USA), I calculated remnant width by averaging remnant width at the camera site (100 m upstream and downstream). I arbitrarily assigned a width of 700 m (more than 100 m wider than the widest linear remnant in my analysis) to cameras placed in native forest near TNNP (i.e., remnants not surrounded by *Acacia* or barren areas). I only calculated remnant length for high-contrast remnant sites, as these sites are most representative of true corridors. I also used Euclidean distance, which is highly correlated with distance via riparian corridors (Spearman correlation, r = 0.97), to measure distance to TNNP from each camera. Given the paucity of animal signs, I assumed that individual animals did not traverse the bare or newly planted land surrounding the high-contrast remnants to reach the sample sites, but rather traveled along the linear remnants. The distance that a species traveled along high-contrast remnants was measured from the point where (1) the land cover on either side of the remnant became denuded or (2) recently planted to the furthest site in the remnant where the species was detected. Based on their location, I assigned each camera site to one of three remnant categories (Figure 4.1), each of which had similar sampling intensity: (1) "high-contrast" remnant (n=17; Figure 4.2 A-C), (2) "buffer-zone" remnant located within 1 km of TNNP (n=17; Figure 4.2 D), or (3) "plantation" remnant, located > 2 km from the national park (n=19; Figure 4.1).

Land-cover covariates

Using ArcGIS, I assigned categories of land cover surrounding each camera based on plantation-company planting maps that were verified by ground-truthing and satellite imagery (Landsat 7 images from 24 Aug 2011 and 30 Dec 2011) recorded during the study in mid-late 2011: (a) native forest, (b) older *Acacia* (5-8 years old), (c) younger *Acacia* (2-4 years old), or (d) barren land (bare soil or newly planted with *Acacia* seedlings), represented by the percent area of each in a 1 km-radius buffer area around each camera. I excluded barren land from my data analyses because of its strongly negative correlation with forest cover (Spearman correlation, r = -0.66).

Data Analysis

I compared mammal species diversity among remnant categories using sample-based rarefaction curves with 95% confidence intervals, constructed using the Chao 1 abundance estimator using the *iNEXT* package (Colwell 2006, Hsieh et al. 2013) in R 3.1.0 (R Development Core Team 2014). This method is used to quantify species diversity of an assemblage using sample-size- and coverage-based integrations of rarefaction (interpolation) and extrapolation (prediction) of Hill numbers (or the effective number of species) (Hsieh et al. 2016). Due to the high sensitivity of species richness estimates to sample size, I standardized accumulation curves by the total number of individuals sampled within each linear-remnant category (Gotelli and Colwell 2001). I conducted an ordination of sites based on their species composition using the Bray-Curtis index, and then compared community composition among remnant categories using nonmetric multidimensional scaling in R. I also conducted a permutational multivariate analysis of variance (MANOVA) using distance matrices to assess effects of landscape covariates.

I elucidated important corridor-design and land-cover correlates (i.e., connectivity with national park, distance to national park, remnant width, extent and age of *Acacia*, extent of native forest; Table 4.1) of species richness using linear mixed-effect models (LMM). I used all detection data, and included 'remnant' as a random factor to account for non-independence of cameras located within the same remnant and with bait as a fixed factor. I also included offsets for the number of nights a camera was active. To

avoid model over-fitting due to the limited size of the data set, I included no more than one landscape covariate per ten samples in a single model and no more than 20 models were run in a model set (Field et al. 2012). I built models representing all possible combinations of covariates, while also keeping the number of covariates in the models ≤ 2 and not combining land-cover covariates or intercorrelated covariates ($r > 0.6$) in the same model. I selected the best-fitting models based on Akaike's Information Criterion (AIC) (Akaike 1974) with all models $\Delta AIC < 2$ being considered useful for inference (Burnham and Anderson 2002). I built LMMs using the lme4 package (Bates et al. 2014) in R.

I investigated how the same set of corridor-design and land-cover covariates (see above) affected habitat use of individual species (Table 4.1). I created single-season occupancy models (MacKenzie et al. 2002) using the program PRESENCE v.6.9 (Proteus Wildlife Research Consultants, New Zealand) to estimate the probability of occupancy (*psi*) and detection (*p*) of a species. When sampling takes place in the absence of a closed sampling period (individuals can move in and out of the study site), and sample units are not based on the home-range size of a species, occupancy rates resulting from PRESENCE models can be interpreted as habitat use (MacKenzie et al. 2004). I partitioned detection histories into two-week sample periods (the length of time that best suited the data) and used to analyze eight species that had 40 or more detections in the two-week data set (20% detection rate or higher).

I used a two-step approach for habitat-use modeling (McClure et al. 2012, Olson et al. 2005). First, I modeled sampling covariates (Table 4.1) using single-covariate models to identify the most influential covariate of detection probability while holding *psi* constant at the intercept (Table C1 in Appendix C). Second, I included the top *p* model with all combinations of selected corridor-design and land-cover covariates (*psi* models) to identify the most important predictors of habitat use (Table C2 in Appendix C). I built the same set of models for species richness (Table C3 in Appendix C). In all models, detection-probability covariates included bait (present/absent), camera set-up (lower/higher), sites located in high-contrast remnants (yes/no), season (dry=July-September; wet=October-January), and remnant (four sampled) as random effects (Table 4.1).

I used weight averaged occupancy rates calculated from PRESENCE models for each species to test the independence of the sample sites using Moran's I test for spatial autocorrelation in the Spatial Toolbox of ArcGIS (version 10, ESRI, Inc., Redlands, CA, USA). The resulting values range from 1 (displaying a complete clustering of detections) to -1 (showing a negative autocorrelation).

Table 4.1 Site and sampling covariates used, respectively, to model mammal habitat use and detection probability for eight species in the study site in Riau Province, Sumatra, Indonesia.

Abbreviation	Name	Description
Site covariates		
AcOld	Percent older *Acacia* (planted between 2004 and 2007) in a 1 km radius from the sample site	Numerical
AcYoung	Percent younger *Acacia* (planted between 2009 and 2010) in a 1 km radius from the sample site	Numerical
Forest	Percent forest in a 1 km radius from the sample site	Numerical
Width	Corridor width (average of width at sampling point and 100 m up and down stream)	Numerical
DistMain	Distance to core habitat (Tesso Nilo National Park)	Numerical
ConnMain	Direct connectivity with core habitat (Tesso Nilo National Park)	Categorical (Yes, No)
Sampling covariates		
Bait	Bait used (Magna Glan)	Categorical (Yes, No)
Set up	Camera position	Categorical (High, Low, Good)
IsoCorr	High contrast remnant (surrounded by bare land or *Acacia* planted <1 year prior to sampling)	Categorical (Yes, No)
Season	Wet (Oct-Jan) or dry (July-Sept) season	Categorical (Wet, Dry)
Corridor	Corridor sampled	Categorical (1-4)

Results

In 3,337 trap days, I recorded 19 mammal species in 895 separate camera detections (Table 4.2). This constitutes about half the terrestrial and semi-terrestrial larger mammal species likely to be present in the study area. The pig-tailed macaque, sun bear, red muntjac, and Malay tapir were the most frequently detected species, both in overall detections and the proportion of cameras that detected them (Table 4.2). Carnivores and the Sunda pangolin were among the least frequently detected species (Table 4.2).

High-contrast remnants

Thirteen of the 19 (68%) mammal species detected in the study were detected in high-contrast remnants, suggesting that mammals are able to use riparian forest remnants of 80 - 320 m width (mean 137 m, SD 45 m) surrounded by barren land (Table 4.2). The tapir, sun bear, pig-tailed macaque, red muntjac, marbled cat, and wild pig were detected at the sites farthest from the national park, up to 3.75 km into one of the high-contrast remnants. Detections were relatively well-spread throughout the length of the remnants showing no correlation between detection frequency and distance into the remnant, with the exception of the tapir which has increasing detections at greater distances into high contrast remnants ($r = 0.61$, $p < 0.05$) (Figure 4.3).

The other six species not detected in high-contrast remnants were detected infrequently elsewhere; the Sunda clouded leopard and binturong were only detected once in the park buffer zone; the Sumatran tiger was detected three times by the cameras (in two of the three connected remnants) although tiger tracks were seen throughout the plantation over the course of the study, often along dirt transit roads and well-used human paths; and the leopard cat, sambar deer, and common palm civet were detected ≤ 8 times. I detected the Asian elephant regularly on transit roads in the plantation through tracks, dung, and company-employee sightings, but never within high-contrast remnants.

Rarefaction curves showed that mammal species diversity was largely similar in high-contrast and plantation remnants (Figure 4.4). Observed and extrapolated species diversity in the national-park buffer-zone remnants was higher than that found in high-contrast remnants and plantation sites, although the 95% CIs overlapped, suggesting this difference was non-significant. Nonmetric multidimensional scaling suggests that differences in mammal community composition among the three remnant categories were not large (Figure 4.5), although species richness was significantly different (pseudo-F value = 2.445; P = 0.002; permutational MANOVA with 1000 randomizations).

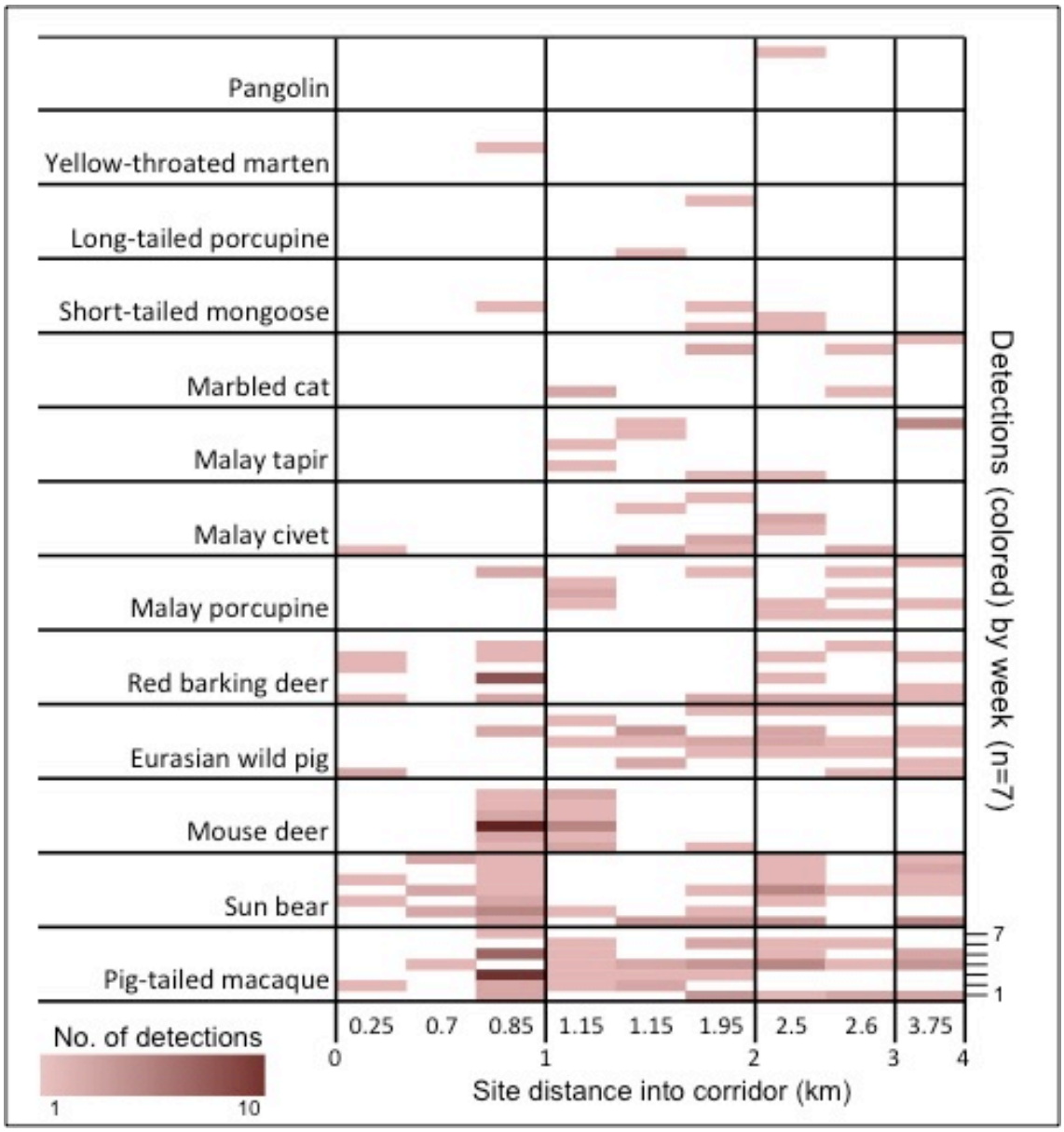

Figure 4.3 Species detections in "high contrast" riparian forest remnants (linear forest remnants roughly 100-200 m wide surrounded either side by denuded land or recently planted *Acacia mangium*) in an *Acacia mangium* plantation in Riau Province, Sumatra, Indonesia. Each distance sampled (represented by 2 cameras spaced c. 50 m apart) is displayed along the x-axis and detection data along the y-axis. Shaded cells indicate that a detection occurred that week; the shade gradient shows a single detection in the lightest shade and the maximum detections recorded (n=10) in the darkest shade. Detections are considered independent if a 30-minute gap exists between the last photo of a series and the first photo of a subsequent series.

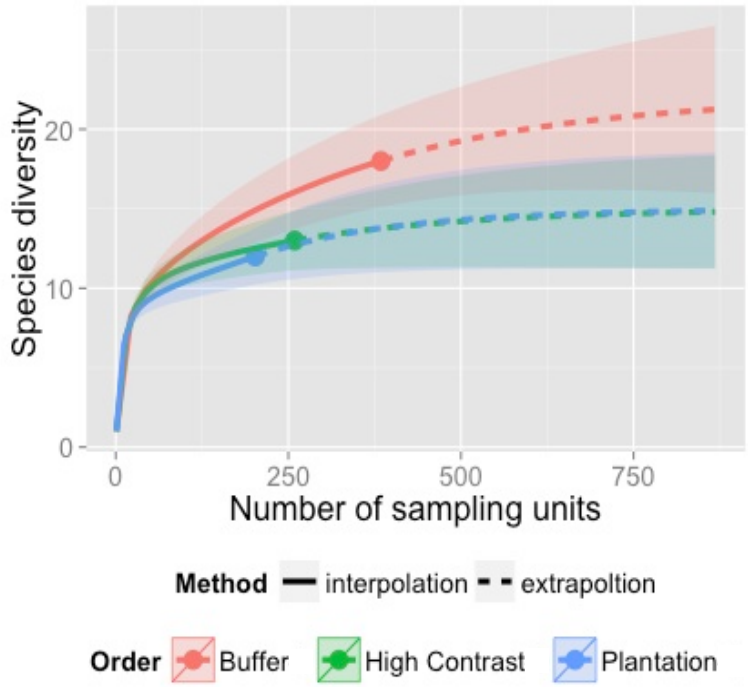

Figure 4.4 Observed (solid line) and extrapolated (dotted line) species diversity at the study site in Riau Province, Sumatra, Indonesia, constructed using sample-based rarefaction curves for Tesso Nilo National Park buffer zone sites (red), sites within the plantation (blue), and "high contrast" remnant sites (green). The x-axis is scaled to show extrapolations up to the same number of individuals sampled in each habitat category. Shading represents the 95% CI for each habitat category.

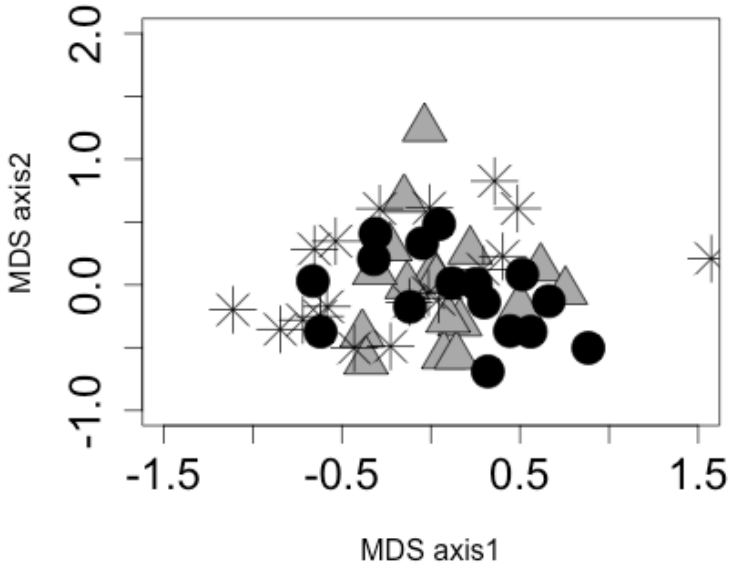

Figure 4.5 MDS graph suggesting minor differences in species composition between landscape categories (buffer, high contrast, and plantation) at the study site in in Riau Province, Sumatra, Indonesia.

Table 4.2 Species detected at the study site in Riau Province, Sumatra, Indonesia, including IUCN Red List category, species diet, and detection frequency statistics in each landscape category.

						Detections per 100 trap days			
Common name	Scientific name	IUCN	Diet	No. of detections	Proportion of sites (n=57)	Plantation (n=19)	Buffer zone TNNP (n=17)	High contrast remnant (n=17)	*Acacia* (n=4)
Pig-tailed macaque	*Macaca nemestrina*	VU	H	185	0.89	3.52	6.47	7.49	3.38
Sun bear	*Helarctos malayanus*	VU	O	143	0.68	3.24	4.64	6.51	0
Red muntjac	*Muntiacus muntjak*	LC	H	106	0.58	1.90	3.90	3.44	4.14
Mouse deer	*Tragulus* spp.	LC	H	99	0.28	0.86	4.98	3.69	0
Malay tapir	*Tapirus indicus*	EN	H	98	0.54	2.38	4.06	1.23	5.26
Malay porcupine	*Hystrix brachyura*	LC	O	85	0.47	2.00	3.73	1.97	1.13
Wild pig	*Sus scrofa*	LC	O	70	0.60	2.00	1.24	3.69	1.5
Malay civet	*Viverra tangalunga*	LC	O	49	0.40	2.66	0.58	1.72	0
Long-tailed porcupine	*Trichys fasciculata*	LC	O	21	0.07	0.00	1.58	0.25	0
Marbled cat	*Pardofelis marmorata*	NT	C	9	0.12	0.00	0.08	0.98	0
Sambar deer	*Rusa unicolor*	VU	H	8	0.12	0.38	0.33	0.00	0
Short-tailed mongoose	*Herpestes brachyurus*	NT	C	7	0.11	0.10	0.08	0.61	0
Common palm civet	*Paradoxurus hermaphroditus*	LC	O	4	0.07	0.10	0.17	0.00	0.38
Leopard cat	*Prionailurus bengalensis*	LC	C	3	0.04	0.00	0.17	0.00	0.38
Sumatran tiger	*Panthera tigris sumatrae*	CR	C	3	0.05	0.10	0.17	0.00	0
Yellow-throated marten	*Martes flavigula*	LC	O	2	0.04	0.00	0.08	0.12	0
Clouded leopard	*Neofelis diardi*	VU	C	1	0.02	0.00	0.08	0.00	0
Binturong	*Arctictis binturong*	VU	O	1	0.02	0.00	0.08	0.00	0
Sunda pangolin	*Manis javanica*	CR	I	1	0.02	0.00	0.00	0.12	0

International Union for the Conservation of Nature (IUCN) Red List Categories: CR = Critically Endangered; EN = Endangered; VU = Vulnerable; LC = Least Concern
C = carnivore, O = omnivore, H = herbivore, I = insectivore

Effects of corridor-design and land-cover covariates

My analysis showed that distance to national park was the strongest predictor of species richness (Table C1 in Appendix C). This covariate was in the AIC-best LMM model although its 95% CI included zero. However, Arnold (2010) suggested using covariates for inference if the 85% CI excluded zero. Therefore, I interpret the results as weak evidence for an effect of distance from the national park.

Of the eight species analyzed using occupancy models, detection probabilities for seven were affected by sampling covariates (Table C2 in Appendix C). The use of bait had a strong positive influence on Malay civet detection ($\beta = 2.26$, SE = 0.59). Cameras set relatively high had a positive effect on red muntjac detection ($\beta = 1.18$, SE = 0.45) and a negative effect on porcupine detection ($\beta = -1.06$, SE = 0.49). High-contrast remnants had a negative influence on tapir detection ($\beta = -1.45$, SE = 0.55) and a positive influence on wild pig and pig-tailed macaque detection ($\beta = 1.02$, SE = 0.39; $\beta = 0.86$, SE = 0.34, respectively). Remnants (four sampled localities) influenced mouse-deer detection probability, with lowest detection in the plantation remnant ($\beta = -2.95$, SE = 1.09) and the highest in the western and central remnants ($\beta = 3.71$, SE = 1.22; $\beta = 3.45$, SE = 1.34, respectively). Season did not appear to affect detection probability for any of the species modeled. There was no significant spatial autocorrelation (Moran's I ranging from 0.01 to -0.11) for the eight species modeled, except the mouse-deer which was clustered (Moran's I = 0.21), having been detected many times at few cameras. Z-scores for all except the mouse-deer were between -1.96 and 1.96, indicating the data was not significantly autocorrelated within a 95% confidence level.

Habitat use of six out of eight species appeared to be affected by corridor-design and land-cover covariates (Table 4.3 and Table C3 in Appendix C). Remnant width and distance to the national park were the most common corridor-design covariates in the top models for each species. Tapir and Malay civet had increased habitat use with wider remnants, whereas sun bear showed an opposite trend. Tapir and red muntjac habitat use increased with increasing distance from the national park, but this relationship was opposite for the Malay civet. Direct connectivity to the national park only influenced habitat use of the Malay porcupine, which increased use with more

direct connectivity. None of the covariates analyzed in the models explained habitat use of the pig-tailed macaque or wild pig (Table 4.3).

Land-cover covariates influenced five of the eight species. Tapir and mouse deer had a positive association with forest cover, but sun bear had a negative association. Malay porcupine had a strong negative association with older *Acacia*, while the red muntjac had a negative association with young *Acacia* (Table 4.4). Although not included in the occupancy modeling, tapirs were regularly detected by the four exploratory cameras placed in old *Acacia* stand.

Table 4.3 Top logistic models for predicting habitat use of eight mammal species based on riparian corridor features in an *Acacia mangium* plantation landscape in Riau Province, Sumatra, Indonesia.

Species	est. naïve *psi*	AIC	ΔAIC		No. Par.	(-2LL)	β	SE
Tapir p(IsoCorr)	0.52							
psi(forest+DistMain)		207.88	0.00	0.2470	5	197.88	4.095	2.08
psi(DistMain+width)		207.98	0.10	0.2350	5	197.98	1.201	0.91
Sun bear p(1)	0.73							
psi(width)		248.44	0.00	0.1884	3	242.44	-0.813	0.43
psi(forest)		249.77	1.33	0.0969	3	243.77	-3.206	2.08
Pig-tailed macaque p(IsoCorr)	0.87							
psi(1)								
Wild pig model p(IsoCorr)	0.80							
psi(1)								
Mousedeer p(corridor)	0.30							
psi(forest)		144.94	0.00	0.1649	6	132.94	0.6390	0.45
Malay porcupine p(setup)	0.48							
psi(AcOld+ConnMain)		191.37	0.00	0.3916	5	181.37	-6.972; 2.773	3.39; 1.50
Red muntjac p(setup)	0.56							
psi(DistMain)		217.69	0.00	0.3484	4	209.69	15.198	18.23
psi(AcYoung)		219.61	1.92	0.1334	4	211.61	-2.701	1.78
Malay civet p(bait)	0.44							
psi(DistMain+width)		148.09	0.00	0.5131	5	138.09		

Table 4.4 Occupancy model beta coefficients (β) showing the strength (slope) and direction of influence of each habitat use covariate on the species analyzed in Riau Province, Sumatra, Indonesia.

Species	Model Occupancy Covariates					
	Forest	Old *Acacia*	Young *Acacia*	Distance to NP	Connectivity to NP	Remnant Width
Tapir	4.09			1.20		0.86
Sun bear	-3.21					-0.81
Pig-tailed macaque						
Wild pig						
Mouse deer	0.64					
Malay porcupine		-6.97			2.77	
Red muntjac			-2.70	15.20		
Malay civet				-9.22		10.43

Discussion

Corridor length and width

The importance of corridor width and length has been little studied in the tropics. This study suggests that many larger mammal species in Sumatra are willing to use linear remnants ranging from 80-530 m in width (with most remnants being 100-200 m in width), traveling at least 3.75 km along these remnants away from core areas of native forest. My findings are broadly similar to studies of Australian arboreal mammals, which suggested that remnant rainforest corridors of at least 200 m in width were desirable (Laurance and Laurance 1999). In Amazonia, it was also suggested that remnants of ~400 m were desirable for mammals (Lees and Peres 2008). The results also fall roughly within recommended corridor widths of 30 – 500 m for temperate forests (Fischer and Fischenich 2000).

Even high-contrast remnants, which were surrounded by a relatively hostile matrix of recently cleared or replanted land, facilitated movement of threatened species and tiger prey species. The Sumatran tiger is of particular importance as a Critically Endangered species central to conservation efforts in Sumatra. Four of the eight IUCN-listed threatened species detected in the landscape (pig-tailed macaque, sun bear, tapir, and pangolin; Table 4.2) and all tiger-prey species (pig-tailed macaque, tapir, sambar deer, mouse deer, wild pig, red muntjac, and Malay porcupine; (O'Brien et al.

2003b)), except the sambar deer, were detected in high-contrast remnants. The four threatened species not detected in high-contrast remnants (clouded leopard, binturong, tiger, sambar deer) were detected infrequently by the cameras. The Sumatran tiger and sambar deer are known to use *Acacia* plantations (McShea et al. 2009); (Sunarto et al. 2012). Tigers are likely opting to travel along areas with better forest and *Acacia* cover (Sunarto et al. 2012) and on larger trails than those sampled (Karanth and Sunquist 2000). The species detected furthest (3.75 km) along the high-contrast remnants (tapir, sun bear, pig-tailed macaque, red muntjac, marbled cat, wild pig) have relatively large home ranges, which may explain their willingness to travel further from native forest.

Remnant width was an important predictor of habitat use for only three of the eight species used in occupancy modeling (all detected in high-contrast remnants), with the tapir and Malay civet favoring wider remnants and the sun bear favoring narrower remnants. Linkie et al. (2013) found that tapir occupancy in regions such as Sumatra increased in areas with a lower human disturbance, a situation more likely to be found in wider remnants. My results indicated that tapirs showed greater habitat use with increasing forest cover (a correlate of remnant width). As the Malay tapir is an important target species for conservation, corridor design in landscapes with this species should focus on creating wider corridors and access to additional forest habitat to accommodate their needs.

Distance and connectivity to core habitat

A number of tropical corridor studies have documented species-specific responses to use of core habitat compared to corridors and a negative response to reduced corridor connectivity (Lees and Peres 2008, Nasi et al. 2008, Parren et al. 2002, Laurance et al. 2008). I found a similar pattern with distance to core habitat being an important covariate for three species (tapir, red muntjac, and Malay civet, although the direction of the relationship differed among species), but less importance on direct connectivity to core habitat. Comparisons among the buffer zone, high-contrast remnants, and plantation-remnant categories showed that the national-park buffer-zone sites (closest to core habitat were the most species-rich; although mammal community composition among the three categories was similar.

Among the species I studied, only the Malay porcupine showed evidence of requiring corridors directly connected to the national park as an important corridor-design covariate. I consider it likely that other species will avoid moving far into an *Acacia* matrix (e.g., sun bear (McShea et al. 2009) and will also likely require a relatively well-connected network of corridors to move throughout plantation landscapes). Species dependence on direct connectivity was probably less important in this study due to the relatively high permeability of the *Acacia* matrix (McShea et al. 2009) and the terrestrial nature of most of the species I studied. Some species, such as the clouded leopard, are unlikely to move far from core habitat forest, regardless of the level of remnant connectivity.

Land Cover

Overall, species use of the *Acacia* plantation I surveyed was relatively high compared to detection rates in plantations in Malaysian Borneo (McShea et al. 2009). This is likely a result of the study site being connected to Tesso Nilo National Park, providing quality source habitat. It may also be a result of individual animals exploring a newly evolving landscape, displaying greater movement rates than would exist as the system approaches equilibrium. Severe poaching and the illegal planting of oil palm in and around TNNP might also have prompted some animals to use the commercial plantation, where signs of hunting activity was much more limited.

The extent of forest cover surrounding a sample site appears to be less important than I initially hypothesized, with only the tapir and mousedeer showing a positive association with increased forest cover. Tapir preference for forest remnants deep inside the plantation and forested areas in the park buffer zone reflects the known willingness of tapir to use degraded and edge habitat (O'Brien et al. 2003b, Maddox et al. 2007), while generally preferring forest over plantations (Maddox et al. 2007). High levels of tapir activity in the plantation, including the use of old *Acacia* stands, may be a result of reduced habitat in TNNP, as well as the proximity of the survey sites near water, in lowland forest, and the apparent absence of tapir hunting in Sumatra (Linkie et al. 2013).

My hypothesis that older *Acacia* stands would be favored over younger stands was supported only for the red muntjac. The Malay porcupine, however, had a negative association with plantation age.

Implications for Conservation

This study suggests that linear riparian remnants can have utility as habitat and potential movement corridors for many larger mammal species in Sumatra, at least for localized movements extending up to a few kilometers in length. The corridors of remnant native riparian forest mostly ranged from 100-200 m in width. I believe this is a reasonable minimum width for riparian buffers to serve as movement corridors for large mammals in Sumatra. Small breaks in connectivity (e.g., service roads) did not appear to be an impediment for most large, terrestrial mammals, though wider breaks in connectivity were more important for some species. The extent that these recommendations are transferable to other agricultural and village settings will depend largely on broader landscape features (such as extent of source habitat), human population density and human activities (especially hunting) (O'Brien et al. 2003a). Large mammal use of linear remnants may also vary between individuals within species depending on prior knowledge of the remnant riparian forest (if it was part of their home range prior to conversion of the surrounding landscape). Individuals that are new to an area might be less willing to use these “high contrast” remnants.

This study is the first to assess the habitat and landscape factors that influence the use of linear remnants by the Malay tapir. I found that that tapir use of linear remnants increases with remnant width and availability of native forest within the remnant. I also found that tapir venture deep into *Acacia* plantations, travelling up to 3.75 km along high-contrast linear remnants, using remnants with greater intensity as they travel farther from core habitat.

The design and management of corridors for mammals in plantation dominated landscapes requires consideration of many factors affecting their suitability. Edge effects could reduce the quality of riparian corridors, especially during harvest rotations when the plantation is temporarily denuded and remnant corridors are more exposed to wind, microclimatic stresses, and additional environmental and

anthropogenic pressures. In neighboring plantations that had experienced multiple harvesting rotations, riparian-forest quality was severely degraded compared to the study area. The impact of biophysical stresses was likely worsened by illegal logging, which I also observed in the study area in corridors where the surrounding *Acacia* had recently been harvested. To maintain habitat quality and corridor functioning in the long-term, the widest possible riparian corridors are recommended to counter edge effects and improve the likelihood of recovery from illegal logging.

Habitat quality and permeability of the land cover surrounding linear remnants should also be considered. Although many mammal species in the study showed a willingness to use forest remnants, the presence of an adjacent *Acacia* matrix may be helpful to enlarge effective habitat for some species of conservation concern. Research into optimal spatial and temporal harvesting rotations that encourage corridor use by large mammals and other native wildlife could improve biodiversity outcomes of plantation management (Lindenmayer et al. 2006). Based on my current knowledge on corridor use and connectivity, harvesting regimes should ensure that plantation areas do not rely solely on long, high-contrast riparian corridors to connect large mammals to core habitat.

Finally, depending on the type of plantation, governance and ownership, connectivity and corridor design issues are often considered post-development and/or in already fragmented landscapes. In situations where riparian buffers are degraded, patchy, or no longer present, reestablishing buffers of 100-200 m of native vegetation is likely to provide passage for many large mammals. Corridors at this width or wider, even when kilometers in length, could play an important role in maintaining landscape connectivity.

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Chapter 5 Modeling species distribution and habitat connectivity with multi-species occupancy models

This chapter is based upon a paper in preparation for submission to Landscape Ecology:

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Statement of contribution of others:

Yaap was the lead author and lead researcher. Tobler was a primary co-author, designing and running the occupancy and connectivity models, and contributing substantially to all sections of this chapter. Broadbent and Zambrano provided GIS data, creating landscape covariate rasters and providing updated land cover maps. Watson assisted with field data collection and data entry. Tobler, Samia E. Carrillo-Percastegui and Esteban Brenes assisted with ocelot and margay species identification. Laurance provided guidance on study design and the manuscript.

Abstract

Biological corridors are often designed to meet the diverse ecological needs of multiple species across a landscape. Methodology on how to best accommodate multiple species within corridor design is an emerging area of research. Using camera trap data and multi-species occupancy models, I evaluated habitat use and distribution of large (>1 kg), terrestrial mammal species across Costa Rica's Osa Biological Corridor. I used circuit-based connectivity analysis to identify critical connectivity areas that link core habitat areas for these species. Of 16 large mammal species analyzed, the majority were found to prefer forest over other habitats sampled: mangroves, oil palm and grasslands and stands of a riverine palm species, *Raphia taedigera*. Although recent studies have suggested that multi-species corridor connectivity scenarios are likely more effective when modeled based on combinations of ecologically similar species, most single-species corridors in the study showed a strong overlap with the multi-species corridor based on the average habitat preference of all species. I believe that my integrated approach of intensive landscape scale sampling with camera traps, multi-species occupancy modeling and corridor modelling is cost efficient and especially useful for defining regional corridors between protected areas at a scale of a few 100 to 1000 km^2.

Introduction

Deforestation and habitat fragmentation in humid tropical rainforests continue to be a major threat to biodiversity conservation (Laurance 1999, Hansen et al. 2008). Agricultural activities and tree plantations are rapidly expanding across the tropics to meet growing human needs for food, wood and fiber (Hansen et al. 2013, Riitters et al. 2016, Haddad et al. 2015, Abood et al. 2015). Such developments are reducing the extent of forests and severing remaining forest blocks, thereby reducing and fragmenting wildlife habitat (Fischer and Lindenmayer 2007, Laurance et al. 2011, Laurance et al. 2002). Large mammals are particularly vulnerable to such habitat loss and fragmentation because of their large area needs and high susceptibility to

poaching and other human induced pressures (Cardillo et al. 2005, Tucker et al. 2018, Laurance 1991).

Biological corridors are a popular conservation strategy used to maintain functional connectivity in fragmented landscapes, increasing gene flow and reducing extinction risk (Wilson and Willis 1975, Diamond 1975, Bennett 2003, Hilty et al. 2006). These days, most corridors are designed by evaluating the cost of movement of a species across the landscape between two or more habitat patches. Popular methods are least cost path or least cost corridor models (Adriaensen et al. 2003, Beier et al. 2008) and circuit models (McRae et al. 2008). Corridors are most often designed to accommodate single wide-ranging species (e.g., tiger, elephant, jaguar) (e.g., Rabinowitz and Zeller 2010, Wang et al. 2014, Dickson et al. 2013, Cushman et al. 2010, Yumnam et al. 2014), usually with the assumption that such an umbrella species will incorporate the needs of less threatened or less charismatic species in the corridor design process (Breckheimer et al. 2014). Although it is generally accepted that broader conservation outcomes can be achieved if corridor design can meet the needs of multiple species (Beier et al. 2008), methodologies on how best to use empirical data to design corridors that accommodate multiple species is still an emerging area of research (e.g., Brodie et al. 2015, DeMatteo et al. 2017, Krosby et al. 2015, Lechner et al. 2017). Challenges faced when designing multi-species corridors include not only data limitations on movement and resource use of each species, but also modeling these data across thematic and spatial scales (Cushman and Huettmann 2010, Zeller 2016) and ensuring adequate habitat for each species within the resulting corridor. Assessing guilds is one approach being used in multi-species corridor modelling (Brodie et al. 2015, Lechner et al. 2017). Some researchers are averaging single-species resistance layers to create multi-species resistance layers within guilds (e.g., Brodie et al. 2015) or across focal species (e.g., Krosby et al. 2015) to model corridors, while others are grouping species by shared dispersal and habitat characteristics and creating a single resistance layer for the group based on expert knowledge of these variables (e.g., Lechner et al. 2017). Comparison of corridors created with the single and multi-species resistance layers can then be undertaken (Brodie et al. 2015, DeMatteo et al. 2017).

Data quality in corridor design has improved substantially over the last decade with GPS telemetry, and genetic data more often used in place of expert opinions to create cost surfaces as the basis for corridor models (Zeller et al. 2016, Epps et al. 2007, Abrahms et al. 2017, Yumnam et al. 2014). However, such data are expensive to obtain and are not available for most species, especially in the tropics. Camera traps are an efficient tool for surveying terrestrial mammals in tropical forests, allowing for detection of rare or elusive species and the collection of data at the community level (Tobler et al. 2008). In combination with occupancy models (MacKenzie et al. 2002) they have been widely used to evaluate wildlife-habitat relationships while accounting for imperfect detection (Linkie et al. 2007, Tobler et al. 2009, Sollmann et al. 2012, Gerber et al. 2012). More recently multi-species occupancy models have been used to model species richness, occupancy, and habitat use of complete mammal communities (Sollmann et al. 2017, Tobler et al. 2015, Burton et al. 2012, Rich et al. 2016, Reilly et al. 2017). Outputs from occupancy models can be used to predict the distribution of species across the landscape analog to species distribution models or resource selection functions (Guillera-Arroita 2017). Assuming that movement costs increase with decreasing habitat quality these species distribution or potential habitat maps can then be used to define cost surfaces for corridor models (Chetkiewicz and Boyce 2009).

The challenge of maintaining connectivity for multiple species across a modified landscape is exemplified in the Osa Biological Corridor on the Osa Peninsula, Costa Rica. Located in Puntarenas Province in the remote southwest of the country, the 1,200 km^2 peninsula is the largest and one of the last remnant lowland forests along Central America's Pacific coast and one of Costa Rica's most biologically diverse and intact ecosystems. The Osa Biological Corridor consists of a collection of forest reserves and private lands that connect the three largest intact conservation areas on the Osa Peninsula: Corcovado National Park (CNP), Piedras Blancas National Park (BPNP) and the Terraba-Sierpe National Wetland (TSNW) (Figure 5.1). The corridor was established to maintain ecosystem functions and evolutionary processes across the Osa Peninsula while maintaining connectivity for multiple, especially wide ranging, species (Jolliffe 2006).

The ecological connection of CNP, BPNP, and TSNW has been a central issue for conservation land managers and non-government organizations (NGOs) working on conservation issues in the region. NGOs and government conservation efforts over the past two decades have focused on identifying the most important areas in the corridor for biological exchange between the two national parks; preventing further deforestation and fragmentation in the corridor and; conserving (often through purchase) strategic blocks of land thought crucial for connectivity. Multiple efforts have been made to identify the most important areas for connectivity on the peninsula, but these efforts have relied exclusively on habitat as proxies for species rather than empirical data on mammal use of the corridor (Obando and Acevedo 2007) (Appendix D).

Costa Rica's National System of Conservation Areas (SINAC) – Osa Conservation Area (ACOSA) identified field-testing of the proposed connectivity routes by Obando and Acevedo (2007) as an important research question to inform management of the Osa Biological Corridor (pers. comm. J.J. Jimenez, June 2012). The goal of this study was, therefore, to: (1) identify the relative importance of five key habitats on the Osa Peninsula for large mammals, (2) understand the spatial distribution of large mammal species in the Osa Biological Corridor, and (3) use these data to (a) provide spatial recommendations for maintaining connectivity between PBNP, CNP and the TSNW for large mammals and (b) test two known corridor design variables (identified in Chapter 2): species habitat use and distance to core habitat areas.

In this study I used a novel approach for designing multi-species corridor at a regional scale by conducting intensive camera trap sampling across the whole study area to evaluate the distribution of 16 mammal species. I assess the habitat preferences of all species using a Bayesian multi-species occupancy model and then use these data layers to design a multi-species corridor that provides spatial recommendations for maintaining connectivity between PBNP, CNP and the TSNW. I evaluated the effectiveness of this corridor for individual species by comparing it to single-species corridors for each species.

Methods

Study Area

The 740 km^2 study area included all parts of the Osa Biological Corridor located directly between the CNP and PBNP, including the Golfo Dulce Forest Reserve (GDFR), Guaymi Indian Reservation, and TSNW (Figure 1.2 and Figure 5.1). The study area represents a landscape linkage between reserves or large natural areas (Category 1 in Chapter 2), as described by Bennett (2003). Such linkages are generally aimed at maintaining a complete representation of biodiversity in a region. The littoral regions of the study area contain mangrove forests including those of the TSNW to the north, and the Gulfo Dulce (a large gulf) to the south. In the south of the study area, there is a mixture of steep, forested terrain (including the BPNP) interspersed with valleys dominated by human-generated grasslands for cattle grazing and areas of oil palm cultivation. The northern-eastern portion of the study area is relatively flat, containing extensive areas of a single naturally occurring wetland palm (*Raphia taedigera*; hereafter referred to as *Raphia*) and grasslands, though some hilly forest areas do exist. The forest is classified as Isthmian-Pacific moist forests (Olson et al. 2001) and the climate is tropical with a mean annual temperature of 24.5–26.5°C and 3.5 –7 m yr^{-1} of annual precipitation. The highest point in the study area is < 800 m a.s.l.

Over half of the Osa Biological Corridor is covered in dense lowland forest, with other naturally forested land covers consisting of secondary forests, mangroves and *Raphia* stands. A mosaic of other human derived land covers and land uses can be found across the remainder of the corridor, including grasslands (for cattle grazing), shrublands, tree plantations (mainly melina [*Gmelina arborea*] and teak (*Tectona grandis*), but also oil palm [*Elaeis guineensis*]), rice and other smallholder agricultural lands. Much of this mosaic of natural forest and human derived land uses are located within the GDFR, which lies directly between CRN and BPNP. The GDFR was established for the production of water, timber, wildlife, forage and recreation, intending to have minimum effect on these resources. Established across private lands, forests in the GDFR are fragmented from recent and historical agricultural development and logging, which are allowed in the GDFR if a management plan is

approved. Hunting is also allowed, with minimal enforcement as compared to the national parks (Carrillo et al. 2000). By contrast, the national parks at either end of the GDFR are on government land and actively managed for conservation purposes, with hunting, agriculture and logging disallowed and greatly reduced compared to the GDFR. They are also much more difficult to access than the GDFR.

The study area is home to roughly 225 terrestrial and freshwater mammal species (Wainwright 2007), including four IUCN Red List threatened species of medium and large mammal: Baird's tapir (*Tapirus bairdii*) and Geoffory's spider monkey (*Ateles geoffroyi*), both Endangered, and the Central American squirrel monkey (*Saimiri oerstedii*) and the white-lipped peccary (*Tayassu pecari*), both assessed as Vulnerable. Five of the country's six cat species are endemic to the peninsula, including the Near Threatened jaguar (*Panthera onca*) and Margay (*Leopardus wiedii*), as well as numerous prey species.

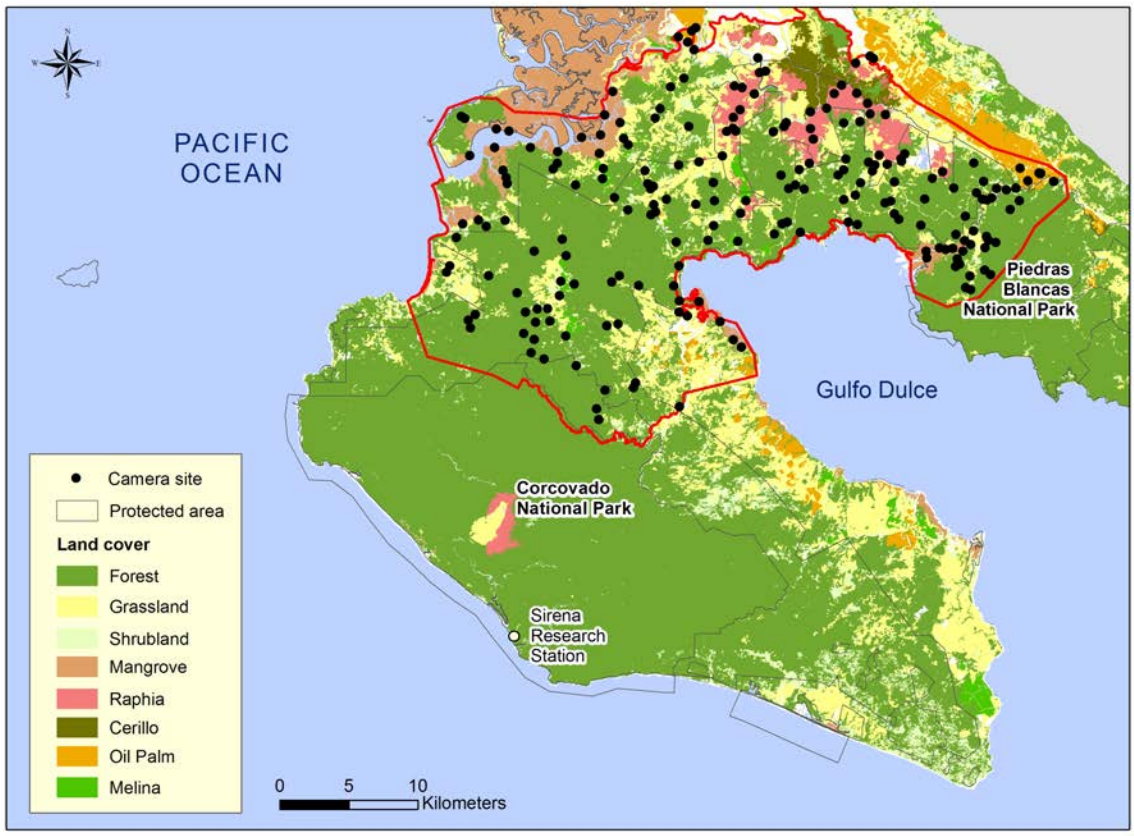

Figure 5.1 Land cover and camera trap sites in the study area (delineated in red) on the Osa Peninsula, Costa Rica.

Survey Design and Camera Trapping Protocol

Over the period February – June 2013, 231 sites across the study area were sampled using camera traps (Reconyx Hyperfire HC 500, Wisconsin, USA). Sampling predominantly occurred within the two dominant land cover types in the study area (1) forest and (2) grasslands, though four less-prevalent land cover types were also surveyed: (3) *Raphia* stands, (4) mangrove forests, (5) oil palm plantations, and (6) melina (grey teak; *Gmelina arboria*) plantations (Table 5.1). Given its importance for mammal species persistence, the majority of sampling occurred in the dominant land cover type, forests. A minimum of 25 sites were sampled in the remaining land cover types, except for melina plantations, where only five sites were sampled. Prior to this study, *Raphia* forests had not been surveyed for mammals in any location, nor had mangrove forests within the study region. Mammal surveys were conducted in oil palm plantations given the recent introduction of this crop and its continuing expansion on the Osa Peninsula. However, the limited spatial extent and infrequent usage (by mammal species) of non-melina timber plantations (e.g., teak, match (*Symphonia globulifera*) and sangrillo (*Pterocarpus officinalis*)) and agricultural crop lands (e.g., rice, banana) resulted in their exclusion from this study.

The study area was sampled using a stratified sampling protocol with the study area divided into twelve zones of approximately 60 km^2 each. The zones guided camera site selection by providing target areas whereby I aimed to have five cameras sites placed in multiple land cover types in each zone at any given time. Camera site selection was then determined by physical accessibility and permission from private landowners on arrival to the target zone. Each site was surveyed using a single camera set at least 100 m into the sampled land cover interior. In drylands, cameras were placed on trees approximately 30 cm from the ground, while in mangrove and *Raphia* they were set at the height necessary to remain above the high-tide waterline but angled downward to ensure detection of species of all sizes. Where possible cameras were set along trails (infrequently used human and well-used animal trails) and in mangrove forests near sighted animal tracks. A thumb-nail sized dollop of scent lure (Ross Carman, Magna Glan, New Milford, PA, USA) was placed in front of each camera, either on a stick

driven into the ground or on an exposed tree root (e.g., mangroves). Cameras were run for a minimum of 28 days before they were moved to a new site.

Spatial data on land cover and anthropogenic factors

Land cover in the study area was derived from the Osa and Gulfito Initiative (INOGO) Mapas land use and land cover data (Broadbent et al. 2013). INOGO Mapas land cover is based on RapidEye satellite images (5x5 m resolution) collected during mid-2012. These data were simplified into seven land cover categories used in the analyses: (1) forest, (2) grassland, (3) oil palm, (4) *Raphia*, (5) mangrove (6) melina, and (7) shrubland (Figure 5.1 and Appendix E).

Based on literature review and prior knowledge, I identified variables likely to affect large mammal habitat and corridor use, and created additional spatial layers to use as covariates for occupancy modeling: tree cover (%), distance to forest (m), distance to nearest large (≥500 ha) forest block (m), distance to each national park (m), slope (degree), elevation (m.a.s.l.), distance to rivers (m), distance to human settlements (m), road density (km/km^2). In addition I evaluated one potential detection covariates: season when the camera was set (wet, dry or transition). Euclidian distance was used to measure distance variables and land cover (%) was calculated by using the percent of each land cover category in a 2.25 ha (150x150 m) area surrounding the camera site from a raster layer in ArcGIS (version 10.4.1; ESRI, Inc., Redlands, CA, USA). All final spatial raster layers had a resolution of 50 m.

Table 5.1. Land covers and their spatial extent in the study area on the Osa Peninsula, Costa Rica. Data include the number of camera-trap sample sites in each land-cover category used in the analysis.

Land cover type	Area (ha)	Percent of total study area	No. of sites sampled (% of sites sampled)
Forest	38,001	51.3%	99 (47%)
Grassland / cattle pasture	14,959	20.2%	29 (14%)
Raphia taedigera	3,145	4.2%	26 (12%)
Mangrove forest	2,577	3.5%	25 (12%)
Oil palm plantation (*Elaeis guineensis*)	889	1.2%	26 (12%)
Other, including timber plantations	6,630	9.0%	5 (2%)
Total	74,027	100%	210

Data Analysis

Occupancy modelling

To model species distributions and habitat preference within the study area I used a Bayesian multi-species variation of the Royle-Nichols occupancy model (Royle and Nichols 2003, Tobler et al. 2015, Yamaura et al. 2012). This model combines data from all species into a single model, allowing parameter estimates for species with sparse data. The Royle-Nichols version of the multi-species occupancy models performs better than the standard version with camera traps that have a high level of heterogeneity (Tobler et al. 2015) and the estimated local abundance was found to be correlated with local density (Linden et al. 2017). Occupancy is related to abundance a by the following formula $\Psi = Pr(a>0) = 1-exp(-a)$.

Several of the occupancy covariates were highly correlated (e.g., forest and tree cover, distance to forest and distance to forest blocks ≥500 ha) and I therefore had to remove some of them from the final model. I also removed covariates that were not significant for any of the species, leaving us with six covariates for the final distribution model: land cover, distance to nearest ≥500 ha block of forest, distance to CNP and PBNP, distance to river and road density. For predicting landscape resistance (see below) I used a model without the distance to CNP and PBNP variables as distance was explicitly modeled in the connectivity analysis.

As all the land cover variables summed to one and the initial models identified forest as a primary predictor of occupancy for most species, I used forest as the reference category for modeling the effects of the other land cover variables. All covariates were standardized to a mean of zero and a standard deviation of one to improve convergence and allow for easier comparison of the effect size. Models were fitted in JAGS (Plummer 2003) through R (R Development Core Team 2015). I ran three chains with 150,000 iterations, a burn-in of 50,000 and a thinning rate of 100. I visually inspected the chains for convergence. Covariates were considered significant when the 95% Bayesian credible interval did not include zero. I used the model results to predict local abundance (interpreted here as habitat preference) and occupancy for the whole study area.

Connectivity modelling

I evaluated connectivity across the study area both with least cost models (Adriaensen et al. 2003, Beier et al. 2008) and circuit models (McRae et al. 2008). These two approaches are often used in parallel, the first to delineate movement corridors and the second one to find areas that restrict flow and might require special attention (McRae et al. 2008). I selected three protected areas as source areas: Corcovado and Piedras Blancas National Parks and the *Raphia* forests of the Terraba Sierpe National Wetland (Figure 1). The mangrove forests of the TSNW are considered important for overall ecosystem functioning and landscape integrity of the peninsula, but due to low occupancy and an aversion to mangrove land cover by all but one mammal species analyzed this area was not included as a source area in the connectivity analysis.

For the least cost modeling I created resistance raster maps for each species and all species combined (averaged values across all species) using the scaled inverse values of the occupancy raster maps so that cells with the highest predicted occupancy had a value of 1 and cells with the lowest predicted abundance a value of 101. Cells that were covered by water were set to a value of 1000, making them barriers. There is evidence of a non-linear relationship between habitat suitability and resistance surfaces, running the risk of overestimating resistance for dispersal and mating movements when modeling corridors based on habitat suitability (Keeley et al. 2017, Trainor et al. 2013). This risk was reduced by sampling all major habitats in the study area and using occupancy data to create the resistance surface, in turn increasing the likelihood of detecting and accounting for species use of non-preferred habitat during dispersal and mating movements.

For the circuit analysis I used the occupancy layers directly as conductivity values. Least cost modeling was done in Linkage Mapper (v1.1.1, McRae and Kavanagh 2017) and circuit analysis in Circuitscape (v4.0; McRae et al. 2014). All the processing of input and output files was done in R (R Development Core Team 2015).

To compare single species corridors and connectivity to multi-species I first analyzed each species individually. I then created a resistance layer for all species combined by averaging the scaled resistance layers for each species. The occupancy analysis showed

that three species had quite different habitat preferences than the rest, these were raccoon, coyote and jaguarundi. I therefore created a second multi-species resistance layer excluding these three species.

For the least cost analysis I looked at several metrics to compare how well the multi-species corridor works for each single species. First I looked at the percent overlap between the multi-species corridor and each single-species corridor. However even if two corridors don't overlap they can be similarly effective for connecting two habitat patches (Beier et al. 2009). I therefore also compared the minimum cost of moving through the multi-species corridor to the cost of moving through the optimal corridor for each species by calculating the increase in cost (%) in using the multi-species model.

For the circuit analysis I compared how well the current-flow for each species across the whole landscape compared to the current-flow for all species combined using a pair-wise Pearson correlation index the full raster datasets.

Results

Twenty-three large and medium-sized native mammal species were detected in the study area over 5,935 camera traps days (Table 5.2). Of the 231 sites sampled, data from 210 sites were included in the analysis; remaining cameras were disturbed by humans or animals or malfunctioned, and hence their data were removed from the analysis. All raccoon detections were analyzed using a single species (Procyon spp.) due to the difficulty of distinguishing between the two species potentially present (*Procyon cancrivorus* and *Procyon lotor*). The agouti (*Dasyprocta punctata*) was the most frequently detected species with over 1000 detections, followed by the raccoon, coati (*Nasua narica*), collared peccary (*Pecari tajacu*) and paca (*Cuniculus paca*), all having hundreds of detections. The tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), puma (*Puma concolor*), jaguarondi (*Puma yagouaroundi*), coyote (*Canis latrans*), and greater grison (*Alouatta palliata*) were amongst the least frequently detected species, all having less than twenty detections. The howler monkey (*Alouatta palliata*) and Neotropical river otter (*Lontra longicaudis*) were only detected once each.

Table 5.2 Number of camera trap detections and detection frequency (number of detections per 100 trap days) for all large mammal species observed in each of the surveyed habitat types on the Osa Peninsula, Costa Rica.

Species	Common Name	IUCN Red List	Forest	Grassland	Mangrove	*Raphia*	Oil Palm	Melina	Habitat
Artiodactyla									
Mazama temama	Red brocket deer	DD	24 (0.84)	-	-	-	-	8 (5.33)	T
Odocoileus virginianus	White-tailed deer	LC	-	31 (4.39)	-	1 (0.13)	-	-	T
Pecari tajacu	Collared peccary	LC	147 (5.15)	-	2 (0.26)	30 (3.98)	8 (1.12)	7 (4.66)	T
Carnivora									
Canis latrans	Coyote	LC	-	3 (0.42)	-	-	1 (0.14)	-	T
Leopardus pardalis	Ocelot	LC	55 (1.93)	4 (0.56)	-	13 (1.72)	12 (1.68)	1 (0.66)	T
Leopardus wiedii	Margay	NT	19 (0.67)	-	-	1 (0.13)	-	-	T, Ar
Panthera onca	Jaguar	NT	12 (0.42)	1 (0.14)	-	-	-	-	T
Puma concolor	Puma	LC	13 (0.45)	-	-	-	-	-	T
Puma yagouaroundi	Jaguarundi	LC	6 (0.21)	-	-	4 (0.53)	-	-	T
Eira barbara	Tayra	LC	60 (2.1)	-	1 (0.13)	-	-	1 (0.66)	T
Conepatus semistriatus	Striped hog-nosed skunk	LC	31 (1.08)	2 (0.28)	-	3 (0.40)	2 (0.28)	-	T
Galictis vittata	Greater grison	LC	4 (0.14)	-	-	-	-	-	T
Lontra longicaudis	Neotropical river otter	NT	-	1 (0.14)	-	-	-	-	Aq
Procyon spp.	Raccoon	LC	31 (1.08)	29 (4.1)	180 (23.65)	77 (10.23)	78 (10.97)	3 (2)	T, Ar
Nasua narica	Coati	LC	220 (7.7)	11 (1.55)	4 (0.52)	82 (10.89)	10 (1.4)	5 (3.33)	T, Ar
Perissodactyla									
Tapirus bairdii	Tapir	EN	6 (0.21)	-	-	-	-	-	T
Primate									
Cebus capucinus	White-faced capuchin	LC	11 (0.38)	4 (0.56)	6 (0.78)	13 (1.72)	3 (0.42)	-	T, Ar
Alouatta palliata	Mantled howler monkey	LC	1 (0.03)	-	-	-	-	-	Ar

Species	Common Name	IUCN Red List	Forest	Grassland	Mangrove	*Raphia*	Oil Palm	Melina	Habitat
Rodentia									
Cuniculus paca	Paca	LC	150 (5.25)	-	4 (0.52)	4 (0.53)	1 (0.14)	5 (3.33)	T
Dasyprocta punctata	Agouti	LC	898 (31.46)	1 (0.14)	12 (1.57)	7 (0.93)	3 (0.42)	6 (4)	T
Cingulata									
Dasypus novemcinctus	Nine-banded Armadillo	LC	80 (2.8)	-	-	1 (0.13)	3 (0.42)	5 (3.33)	T
Pilosa									
Tamandua mexicana	Tamandua	LC	30 (1.05)	3 (0.42)	3 (0.39)	12 (1.59)	6 (0.84)	-	T, Ar
	Total		1798 (62.93)	90 (12.75)	212 (27.86)	253 (33.6)	127 (17.86)	41 (27.33)	

IUCN Red List categories: EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient
Habitat categories: T = terrestrial; Ar = arboreal; Aq = aquatic

Occupancy and habitat preferences

Twelve out of the 16 species included in the occupancy model showed a significant relationship with some of the covariates (Table 5.3 and Appendix F). The remaining four, jaguar, puma, tapir and coyotes, had sparse data but they still showed clear patterns. The majority of species had a significant negative response to increasing grassland, mangrove, and oil palm cover and therefore a positive response to forest. Conversely, raccoons showed a strong positive response to increasing mangrove cover. There were no significant mammal responses to either Melina or *Raphia* land cover types, other than a significant negative response by agouti to *Raphia*. Raccoon, agouti and nine-banded armadillos increased significantly with increasing shrubland, a land cover type not directly sampled with cameras.

Four species, tayra, paca, agouti and nine-banded armadillos, significantly decreased in occupancy in response to increasing distance to large blocks of forest (≥500 ha) and most other species except for raccoon and jaguarundi also showed a negative relationship. Both collared peccary and agouti occupancy declined significantly with increasing distance from Piedras Blancas NP while red brocket deer, jaguar, puma and tapir declined with distance from Corcovado NP, although not significant. Five species significantly increased in occupancy with proximity to rivers: collared peccary, raccoon, coati, paca and agoutis. Further, both the collared peccary and coati showed a significant increase in occupancy with increasing proximity to roads.

Sampling season affected detection probability for five of the 16 species analyzed (Appendix F). Agouti, nine-banded armadillo, coati, jaguar and ocelot were all easier to detect in the wet season when compared to both the dry season and the transition period between the two seasons. This seasonal effect was strongest in jaguars.

Individual species distribution showed similar patterns for most species with forest presence being a clear driver of positive occupancy for most species (Figure 5.2). Of the species examined, the agouti and coati had the highest occupancy probability across the study area whereas the jaguar and tapir had the lowest. Meanwhile, in the study area, the ocelot, collared peccary and paca were most likely to occur in Piedras Blancas NP. Puma, jaguar, tapir and red brocket deer were predicted to be more

prevalent inside and near Corcovado NP. The raccoon mainly occurs in the north where mangroves are common while the coyote and the jaguarundi almost exclusively occurred in a small area in the north where forest cover declines and the study area borders large expanses of and agricultural lands.

Table 5.3 Beta coefficients (β) for the Royle-Nichos multi-species occupancy model for the study site on the Osa Peninsula, Costa Rica. * indicates significant coefficients (95% credible interval does not include zero). The full table with credible intervals can be found in Appendix F.

Species	Dist. PNC	Dist. PNPB	Shrubland	Grassland	Mangrove	Melina	Oil Palm	Raphia	Dist. Forest 500	Dist. Rivers	Dens. Roads
Agouti	-0.035	-0.256*	0.093*	-0.886*	-1.046*	-0.12	-0.662*	-0.282*	-1.434*	-0.187*	-0.072
Armadillo	-0.061	0.030	0.107*	-0.928*	-1.328*	-0.089	0.047	-0.211	-1.186*	-0.073	-0.110
Coati	-0.034	-0.215	0.089	-0.449*	-0.883*	0.000	-0.537*	0.074	-0.318	-0.201*	-0.252*
Coyote	-0.044	-0.173	0.098	-0.049	-0.871	-0.068	-0.603	-0.184	0.125	-0.177	-0.168
Red brocket deer	-0.255	-0.092	0.102	-0.822*	-1.087*	0.090	-0.621	-0.238	-0.755	-0.167	-0.274
Jaguar	-0.158	0.064	0.097	-0.424	-0.904	-0.087	-0.551	-0.169	-0.696	-0.120	-0.244
Jaguarundi	-0.088	-0.071	0.09	-0.43	-1.033*	-0.087	-0.672	-0.076	0.295	-0.192	-0.26
Margay	-0.102	-0.111	0.101	-0.696*	-0.630	-0.118	-0.700	-0.27	-0.085	-0.103	-0.192
Ocelot	0.082	-0.196	0.087	-0.331	-0.592*	-0.092	-0.290	-0.152	0.001	-0.153	-0.131
Paca	-0.083	-0.238	0.096	-0.720*	-0.704*	-0.045	-0.768*	-0.159	-1.257*	-0.208*	-0.207
Collared peccary	0.111	-0.486*	0.097	-0.708*	-1.277*	-0.081	-0.689*	-0.061	-0.291	-0.225*	-0.294*
Puma	-0.174	-0.028	0.091	-0.580	-0.423	-0.102	-0.588	-0.203	-1.027	-0.113	-0.285
Raccoon	-0.093	-0.147	0.100*	-0.011	0.507*	0.09	-0.003	0.013	0.385*	-0.368*	-0.066
Skunk	-0.100	-0.087	0.092	-0.641*	-1.217*	-0.028	-0.702*	-0.062	-0.313	-0.110	-0.163
Tapir	-0.159	-0.068	0.108	-0.606	-0.868	-0.079	-0.548	-0.178	-0.692	-0.178	-0.234
Tayra	-0.048	-0.134	0.097	-0.766*	-0.519	-0.083	-0.691*	-0.163	-1.298*	-0.125	-0.163

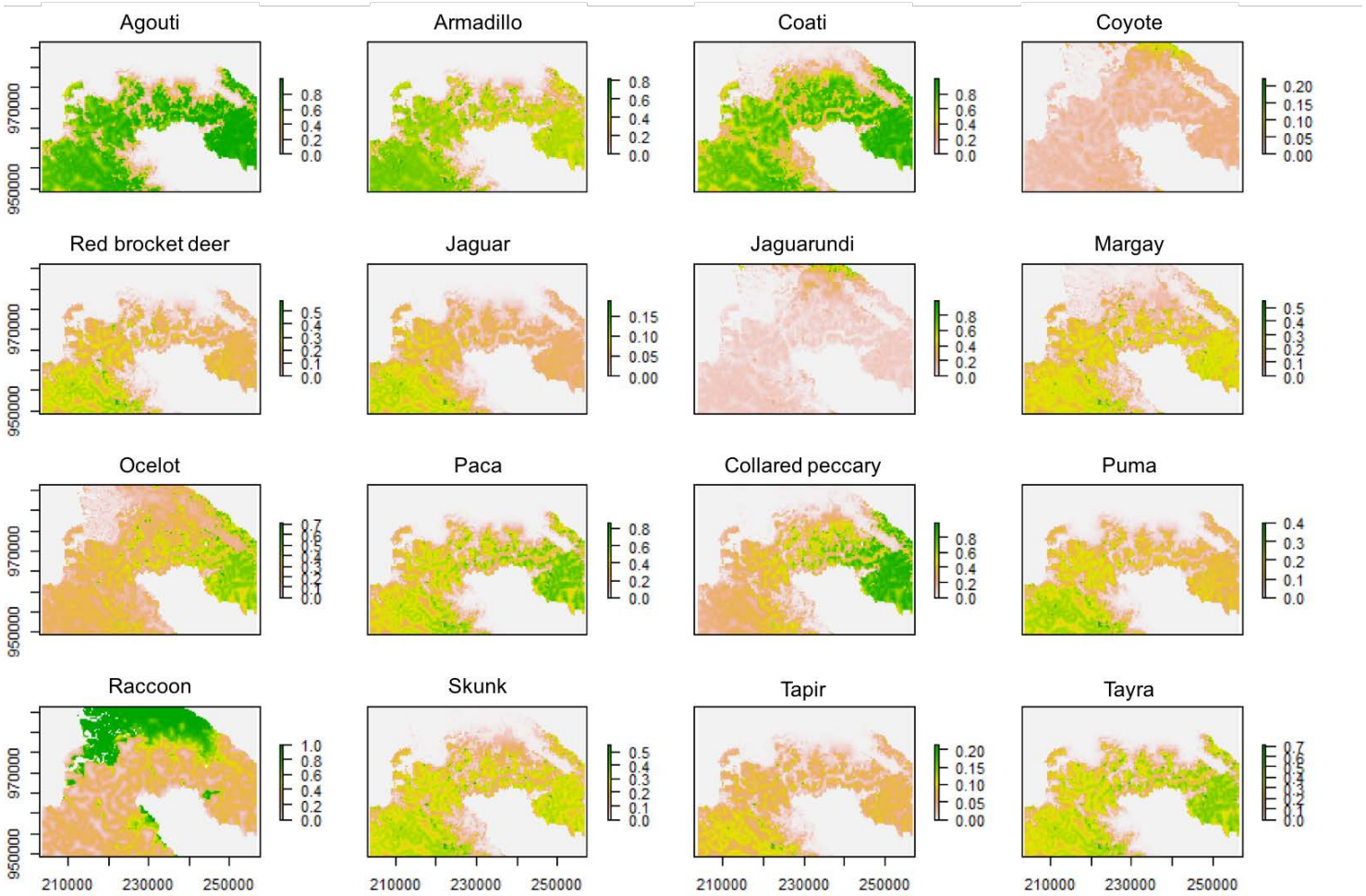

Figure 5.2 Species distribution maps of the study area based on multi-species occupancy models for 16 large mammal species, Osa Peninsula, Costa Rica. Predicted occupancy for each species is displayed with the color-coded legends. The x and y axes display Universal Transverse Mercator (UTM) geographic coordinates.

Connectivity modelling

The corridor analysis identified the main corridors connecting the protected areas. These largely coincide with the areas of high current flow (areas that are most important for animal movement and maintaining connectivity between core areas) identified by the circuit analysis (Figure 5.3). Important mammal movement areas were concentrated in the east of the study area, close to Piedras Blancas NP and the *Raphia* forests of Terraba Sierpe NW, although movement areas were also dispersed sparsely across the west of the study area (Figure 5.3).

The areas in the landscape that facilitated population connectivity were consistent across species (Table 5.4). The optimal corridor for most species had an 85-95% overlap with the multi-species corridors. The coati, coyote, and jaguarundi had a lower overlap of 70-80% and the agouti had only a 64% overlap. The raccoon had an overlap of less than 10%. The agouti is a habitat generalist that can likely find more efficient corridors through habitat unsuitable for other species and the raccoon is a habitat specialist affiliated with water and mangroves, not forest as most other species. For most species the multi-species corridor did not increase cost, or increased cost by a few percentage points with the exception of the raccoon and the agouti which showed larger increases (Table 5.4). The multi-species current map was highly correlated with the single-species maps for most species (>0.90). Again, the coyote, jaguarundi and raccoon had smaller correlations. Removing those three species from the multi-species corridor increased overlap and correlation for most forest species but decreased it for the three excluded species, however, the effect was small.

Table 5.4 Comparison of single species and multi-species corridors modeled for the Osa Peninsula study site in Costa Rica. Each single-species corridor was compared to the multi-species corridor.

Species	Overlap (%)[a]	Overlap sub (%)[a,d]	Cost increase (%)[b]	Cost increas Sub (%)[b,d]	Correlation[c]	Correlation SUB[c,d]
Agouti	63.1	64.0	7.43 (0.00-52.79)	7.43 (0.00-52.79)	0.924	0.968
Armadillo	86.0	86.1	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.914	0.960
Coati	74.2	74.5	0.35 (0.00-3.18)	0.35 (0.00-3.18)	0.970	0.975
Coyote	71.4	69.3	0.43 (0.00-2.68)	0.43 (0.00-2.69)	0.889	0.822
Red brocket deer	90.8	89.5	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.931	0.973
Jaguar	92.7	91.3	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.956	0.989
Jaguarundi	73.0	71.2	0.30 (0.00-2.49)	0.31 (0.00-2.57)	0.880	0.812
Margay	91.9	91.1	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.982	0.988
Ocelot	88.0	86.0	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.973	0.936
Paca	88.5	89.2	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.934	0.976
Collared peccary	84.1	84.1	0.08 (0.00-0.69)	0.08 (0.00-0.69)	0.969	0.987
Puma	93.5	92.8	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.936	0.974
Raccoon	6.8	6.5	22.89 (0.00-68.47)	27.36 (0.00-68.47)	0.616	0.491
Skunk	93.9	93.1	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.970	0.994
Tapir	94.8	91.4	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.952	0.988
Tayra	92.0	92.5	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.927	0.970

[a] Perecntage the single species corridor overlaps the multi-species corridor. [b] Percentage increases in cost for a species when travelling through the multi-species corridor compared to the best single-species cocrridor, mean and range for all linkages. [c] correlation between the current flow map for a single species and the map for all species.
[d] Values for a multi-species corridor with forest species only.

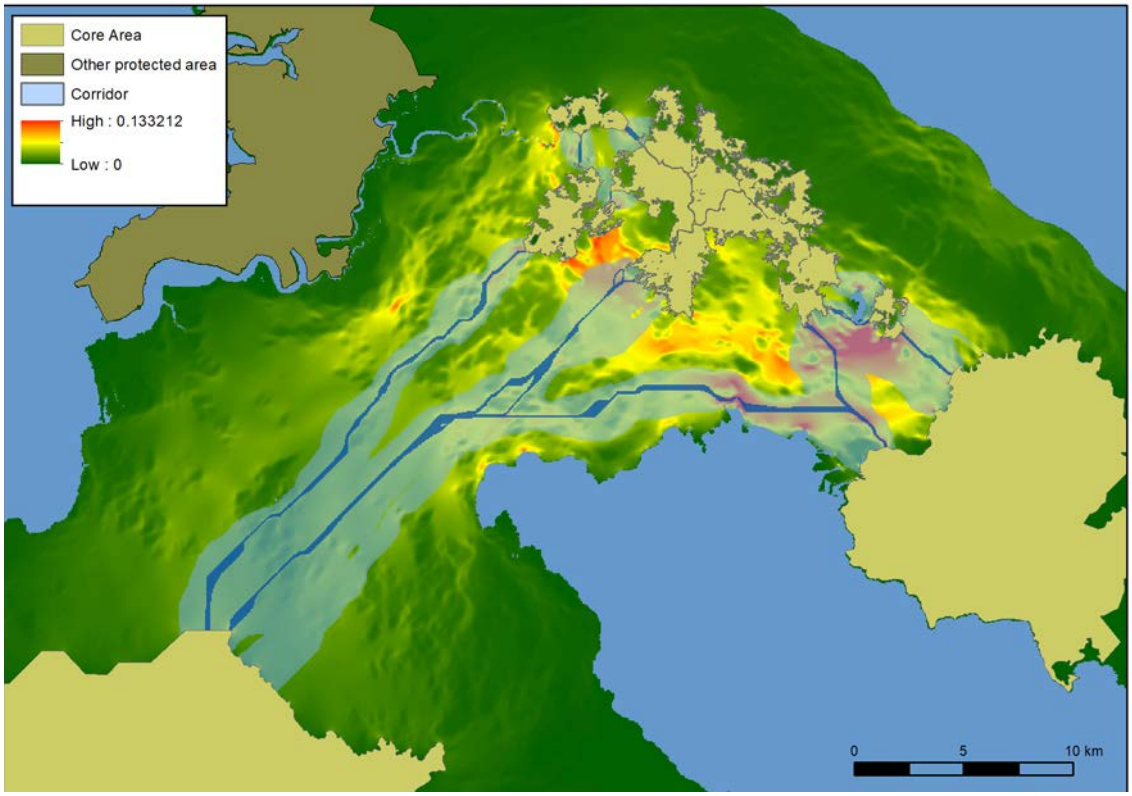

Figure 5.3 Circuit flow analysis using averaged current across all mammal species analyzed in the study area on the Osa Peninsula, Costa Rica. The map shows high-current (red) areas where flow is highest - areas that are most important for species movement to maintain connectivity between core areas. Flow is reduced in yellow and green areas, reflecting either greater availability of the habitat or that areas are not important for connectivity between the identified core areas. The least-cost corridor for all species is overlaid in blue.

Discussion

This study shows that camera traps can be an efficient tool for assessing the distribution and habitat preferences of mammals at a regional scale, forming the baseline for the design of movement corridors. Most of the mammal species found on the Osa Peninsula were forest specialist, something that was clearly reflected by the results from the occupancy models. Grassland and Mangrove habitats were strongly avoided and distance to forest blocks had a negative impact on occupancy. This is not surprising given that tropical moist forest is the main native habitat for this region. Only the raccoon, the coyote and the jaguarundi showed clearly different habitat preferences. Raccoons were associated with mangroves and rivers while coyotes (a

recent immigrant to the area) and jaguarundi were found more frequently close to agricultural land.

The similarity in habitat preference across most species was also evident in the results from the corridor design. Most single-species corridors showed a strong overlap with the multi-species corridor that was based on the average habitat preference of all species. Likewise, there was a minimal change in cost for most species when traveling through the multi-species corridor compared to their optimal single species corridor. This means that a single corridor design can potentially serve the majority of mammal species on the Osa Peninsula.

This is not always the case. A study on multi-species corridors in Malaysia conducted in a landscape 100 times the size of this study area found that corridor connectivity scenarios are likely more effective when modeled based on combinations of ecologically similar species (e.g., carnivores, herbivores) (Brodie et al. 2015). Similarly, a study in Australia found that modeling species corridors by guilds (species with similar habitat preferences and dispersal behaviors) resulted in better corridor designs across species (Lechner et al. 2017). Yet other studies have found that carnivores were poor umbrella species to protect connectivity of other species (Cushman and Landguth 2012, Beier et al. 2009), showing the need for multi-species corridor designs.

While ideally corridor designs would be based on high-resolution data from GPS collars that allow for a much more detailed modeling of resource selection and resistance to movement (Zeller et al. 2016, Abrahms et al. 2017, Cushman et al. 2014), these kinds of data are not available for most species and difficult and expensive to collect. Even in countries such as the United States where GPS collars are more widely deployed for wildlife management projects, data is usually only available for a hand full of species at best (e.g. Fleishman et al. 2017). In the tropics where medium and large-sized mammal communities are more diverse, it is unfeasible to collect GPS telemetry data on even a third of the species.

Camera traps provide a cost efficient method for collecting data on the presence and resource selection of the whole community. With the advances in camera trap technology and the decrease in equipment costs over the last decade, several hundred

sites can now be sampled in a few months at a cost lower than what it would take to equip 10 animals with GPS collars. I agree that the data quality obtained from camera traps is not comparable to telemetry data and there is likely confusion between habitat used by resident animals and dispersing animals (Abrahms et al. 2017), but at the same time camera traps can provide information at the community level that other methods cannot. I therefore see this as a trade-off between designing a single species corridor based on high-quality telemetry data or designing a multi-species corridor based on data of lower quality. Which method is better suited depends on the main objectives of a particular project.

I think that the integrated approach of landscape scale sampling with camera traps, multi-species occupancy modeling and corridor modelling I have used is especially useful for defining regional corridors between protected areas at a scale of several 100 to 1000 km^2. At this scale most of the landscape where the potential corridor will be located can be sampled, giving a good idea of the current distribution of species. Camera traps are less suited for sampling already highly fragmented landscapes and low density species that rarely disperse. In those cases, GPS collars or genetic methods have a better chance of defining connectivity (Zeller et al. 2016, Yumnam et al. 2014). Camera traps can still be used to confirm the use of those corridors by targeted species (LaPoint et al. 2013).

Implications for the Osa Peninsula

This study identified clear priority areas for retaining connectivity for large mammals across the Osa Biological Corridor as well as species specific management issues. High-current areas (red in Figure 3) were predominantly located in the east of the study area showing that the greatest risk to landscape connectivity lies in the east. Of particular importance is the high-current area located in the GDFR along the southern boundary of the study area that coincides with the modeled least cost path corridor. Connectivity between PBNP and CNP will likely rely heavily on maintaining forest in this area. Located between the Gulfo Dulce and the main road that runs east-west across the Osa Peninsula, this stretch of forest is largely inhabited by environmentally-conscious private residents and eco-resorts, but small areas of oil palm are also

present. The continued presence of large mammals in this stretch of forest will be an indication of landscape connectivity being maintained across the Osa Biological Corridor, though GPS telemetry and genetic studies would be necessary to confirm this. Hunting is a threat across the Osa Biological Corridor and could severe connectivity at any point in the landscape, though hunting in high-current areas (such as this location) will likely have a disproportionately large impact on landscape connectivity.

Likewise, one stretch (approximately 3-kilometer in length) of lowland forest remaining on either side of the Esquinas River is expected to be important for connectivity between PBNP and the Osa Peninsula. This high-current area is the only location to connect PBNP with the Osa Peninsula with a continuous stretch of forest. The remaining areas consist of Mangroves, Oil Palm and Grasslands, all identified as poor habitat for most large mammal species. Forests following the high-current path from the forest located along the south of the main road (discussed above) through to PBNP include this 3-km stretch and should therefore also be prioritized for active management and monitoring. This high-current path diverges from the LCP corridor (Figure 3), illustrating the value of using both circuit flow analysis and LCP modeling to understand landscape connectivity.

The majority of remaining high-current areas connect *Raphia* to forests, highlighting the risk of this ecosystem becoming functionally disconnected from the remainder of the Osa Biological Corridor for species that are not willing to traverse expanses of grassland. Although numerous large mammals were detected using *Raphia*, mammal abundance in *Raphia* is dependent on distance to forest. Although *Raphia* stands may play a role in maintaining landscape connectivity (e.g., providing an alternative pathway across the landscape), its connectivity value is expected to be far secondary to a forest dominated corridor for most mammals.

Some species had large variations in occupancy across the study area, warranting further investigation. The puma, jaguar, tapir and red brocket deer all showed higher occupancy in the west, whereas the ocelot and collared peccary were more abundant in the east (Figure 2). Hunting is a plausible explanation for some of the skewed distribution patterns (Carrillo et al. 2000). These patterns should be further

investigated to determine whether populations of these species are indeed in decline and, in the east of the study area, whether declines are an artefact of isolation and severed connectivity with CNP. The abundance of collared peccary in PBNP is also of particular interest because of the close proximity of PBNP to roads and extensive areas of human settlements. PBNP may be providing a better protective function for this species than the GDFR (where collared peccary abundance declined) by way of more active management and limited road access into desirable hunting areas in PBNP. Hunters can easily access the GDFR, including the high-current areas discussed above, by driving along the main road. These variations in abundance require further investigation to ensure that landscape connectivity via the Osa Biological Corridor is not serving as a population sink for some species (Harrison 1992).

Conclusion

Species-specific variation in habitat use was evident in the study, but due to the importance of forest for most large mammal species on the Osa Peninsula, forest habitat had the largest influence on modeled connectivity in the corridor. Priority areas for targeted conservation efforts have been identified based on predicted movement paths. Knowledge gained from sampling and modeling large mammal use of non-forest habitats will also be useful at a finer scale, when land managers need to understand the permeability of different land covers by different species. A major strength of this study was its sole reliance on empirical data collected from camera traps and accurately up-to-date, high resolution land cover data. These factors allow for a high level of confidence in the outcomes.

Chapter 6 Mammal use of *Raphia taedigera* palm stands on Costa Rica's Osa Peninsula

This chapter is based upon a paper published by Yaap et al. (2015), with minimal format and content edits:

Betsy Yaap[a], Haley Watson[b] and William F. Laurance[a]. 2015. Mammal use of *Raphia taedigera* stands on Costa Rica's Osa Peninsula, Mammalia. Volume 79, Issue 3, Pages 357–362.

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Statement of contribution of others:

Yaap was the lead author and lead researcher (study design, field data collection, data analysis and interpretation). Watson played a major role in field data collection and data entry and reviewed drafts of the manuscript. Laurance provided guidance on study design and analysis and reviewed and edited the manuscript.

Abstract

Raphia taedigera is a wetland palm species that occurs in monospecific stands in Central and South America, Africa and Madagascar. Use of this ecosystem by wildlife is largely unknown. I surveyed *R. taedigera* stands on the Osa Biological Corridor in Costa Rica with 26 camera traps to identify which large (>1 kg) mammal species use this habitat and the distance each species will travel into it from surrounding habitats. I conclude that *R. taedigera* provides habitat and a connectivity function in the Osa region for coati (*Nasua narica*), raccoon (*Procyon sp.*), collared peccary (*Pecari tajacu*), white-faced capuchin (*Cebus capucinus*), ocelot (*Leopardus pardalis*), northern tamandua (*Tamandua mexicana*), and paca (*Cuniculus paca*). Other species were only detected on the edges of stands or not at all. Based on a literature review, interviews with farmers, frequent detections of collared peccary, and detection in adjacent habitat, the jaguar (*Panthera onca*) is also expected to traverse *R. taedigera* stands. *R. taedigera* can be considered an important habitat for maintaining connectivity across the Osa Biological Corridor and potentially provide a similar function in other Neotropical landscapes.

Introduction

Raphia taedigera is a riverine palm species that occurs in monospecific stands in South America (Brazil and Columbia), Central America (Costa Rica, Nicaragua, and Panama), Africa and Madagascar (Henderson et al. 1997). It is the only palm in its genus to occur outside of Africa. This species is found in inundated estuarine habitats in close proximity to mangrove forests and establishes itself further inland along tidal river channels. The palms grow up to 20 m tall and produce 15-20 m long pinnate leaves and scaly, egg-shaped fruits approximately 4 x 7 cm in size (Jones 1995, Carney and Hiraoka 1997). Though regularly inundated, these wetland palm forests are not deep enough to be passable by canoe or boat and are difficult to traverse on foot due to porous alluvial soils and areas of open water. Although *R. taedigera* has numerous human uses in some regions (e.g., cooking oil, pig feed, shrimp and fish traps, medicinal, and household construction in Brazil) (Carney and Hiraoka 1997), very limited information is available on wildlife use of this ecosystem.

Methods

As part of a research project investigating large mammal habitat use in the Osa Biological Corridor on the Osa Peninsula of Costa Rica, I sampled *R. taedigera* stands (referred to as *Raphia* hereafter) using automatic camera traps (Reconyx Hyperfire HC 500, Wisconsin, USA). I contrast the mammal assemblage in *Raphia* (n=26) with that in other local habitats, including lowland rainforest sites (n=105), mangrove (n=25), and three manmade habitats: pasture or grasslands (n=30), oil palm (*Elaeis guineensis*) (n=26), and grey teak (*Gmelina arborea*) (n=5). Habitat use in this paper is inferred on the basis of presence data from individual trap locations. By combining data from multiple cameras within any habitat type, a general picture of degree to which that habitat is used by each species was inferred.

In total, 211 sites were sampled across approximately 800 km^2 of the peninsula (Figure 6.1). The study area in this chapter is part of a landscape linkage located between reserves or natural areas (Category 1 in Chapter 2), described in further detail in the Methods section of Chapter 5. From February through June 2013 each site was sampled with one camera for approximately 28 days. The twenty-six *Raphia* sites were spread across the 40 km^2 of *Raphia* forests in the study area. Cameras were placed inside the *Raphia* stand, 25 -1500 m (mean 335 m, median 150 m) away from the edge. Edges were defined as areas where the *Raphia* gave way to a different land cover, most often marshy, herbaceous vegetation, grasslands or well-drained lowland rainforest (Figure 6.2). Site selection was based on river and land access and maintaining a 1 km distance between sites. Cameras were baited with a scent lure (Ross Carman, Magna Glan, New Milford, PA, USA).

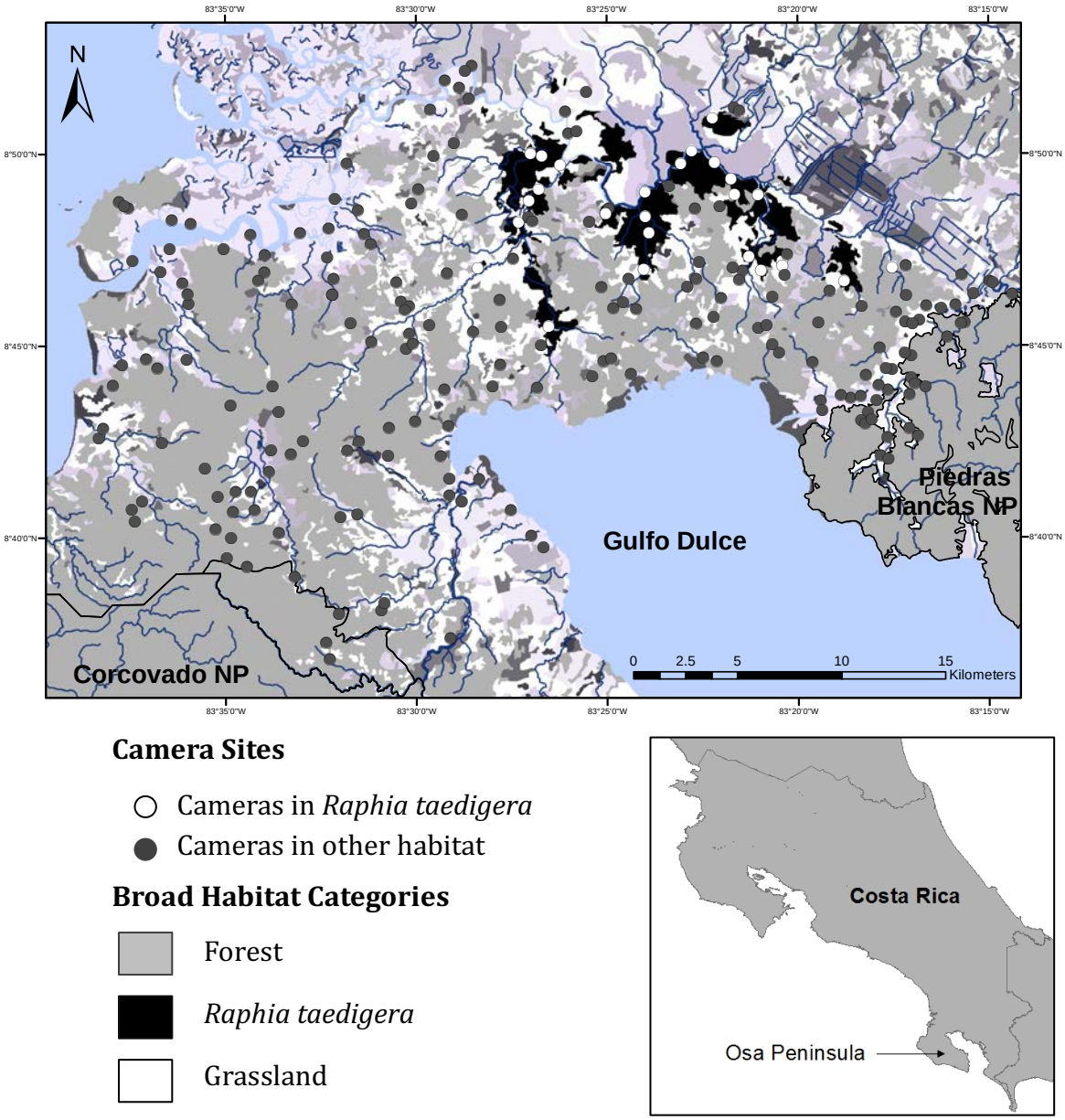

Figure 6.1 Map of *Raphia taedigera* (black) sample sites (white dots) on the Osa Peninsula, Costa Rica. The dominant grey area is well-drained lowland rainforest and the white areas are grasslands. Mangroves are displayed in light grey, predominantly in the NW coastal area of the map. Gray dots are sample sites in other land covers.

Figure 6.2 Photos of *Raphia taedigera* stands on the Osa Peninsula, Costa Rica. Top left: View from a pastureland hillside looking down at a large *Raphia taedigera* stand. The edge where pastureland meets the *R. taedigera* is visible, as well as the forested mountains in the background, where the *R. taedigera* stand ends; Right: Field team walking into a drier stand of *R. taedigera* that lacks a closed canopy. Bottom left: *R. taedigera* growing on both sides of the Sierpe River.

Results & Discussion

Thirteen large mammals (> 1 kg) and a number of small mammals (Sciuridae, Muridae and an opossum) and birds were detected in 753 trap days of *Raphia* sampling (Table 6.1 and Figure 6.3). No humans were detected. A domesticated dog was detected at one site on eight occasions. This camera was approximately 100 m from a farm and the dog was likely attracted to the scent lure.

The large mammals detected constitute close to half of the 23 species detected in the overall study. The coati (*Nasua narica*), raccoon (*Procyon sp.*) and collared peccary (*Pecari tajacu*) were the most frequently detected species, followed by the white-faced capuchin (*Cebus capucinus*), ocelot (*Leopardus pardalis*) and northern tamandua (*Tamandua mexicana*). For each of these species a multiple regression analysis was used to determine the influence on detection frequency of (1) distance from nearest

edge and (2) distance from well-drained lowland forest. Neither of these variables was statistically significant for any species. All six species were detected at least 1 km into *Raphia* on occasion suggesting that they use *Raphia* as primary habitat, and do not simply enter the edges while staying close to other preferred habitats (Figure 6.4).

Interestingly, the coati, tamandua and capuchin were detected at a higher percentage of cameras in *Raphia* than any other habitat sampled (for example, 31% of *Raphia* cameras detected coati, whereas only 12% of mangrove cameras detected this species; other habitats had even lower percentages). For the capuchin and tamandua this could be a result of more time spent on the ground in *Raphia* than other habitats due to a less navigable palm canopy. *Raphia* may be a preferred habitat for coati.

The collared peccary was detected at a similar percentage of *Raphia* cameras (42%) as forest cameras (43%). Capuchins and peccary are known to eat *Raphia* fruit (Wilson 1983, Carrillo et al. 2002, Eadie 2012). *Raphia* stands were fruiting at the time of sampling and this likely accounts for the occurrence of capuchins and peccary in this habitat, but no species was photographed eating the fruit. Mangrove was the preferred habitat for raccoons (100%), but *Raphia* (58%) and grey teak (60%) also had a high percentage of cameras detecting the species. Ocelot detections in *Raphia* were similar to those in grasslands and oil palm (<20%), while grey teak (40%) and forest (30%) had the highest percentage of cameras detecting this species.

The agouti (*Dasyprocta punctata*) was only detected at two *Raphia* sites, one located approximately 60 m from secondary forest and the other 150 m from pastureland. Agoutis are known to prefer forest habitats, but also use gardens and plantations (Reid 1997). *Raphia* is not likely a preferred habitat given that agoutis were detected at a much higher percentage of forest and gray teak sites than *Raphia* (8% of *Raphia* versus 88% of forest and 100% of grey teak) and remained near the edges.

The striped hog-nosed skunk (*Conepatus semistriatus*) was detected at two sites; on two subsequent days at a site located 150 m from the edge of pastureland and once at a site 300 m from a forest edge, 650 m from grassland and 160 m from a hog plum swamp forest (requiring a 30 m river crossing). Home ranges for this species have been known to extend to 53 ha (Walker 2004) allowing for the possibility that the

individuals detected were using *Raphia* in combination with other habitats. Forest cameras detected this species most frequently (18% of forest cameras compared to 8% of *Raphia*, 8% of oil palm, 4% of grassland cameras).

Four species were only detected at a single site: the margay (*Leopardus wiedii*), paca (*Cuniculus paca*), nine-banded armadillo (*Dasypus novemcinctus*), and white-tailed deer (*Odocoileus virginianus*). The margay was detected at one *Raphia* site in the far east of the study area, at a camera site that was largely surrounded by *Raphia* and grassland but approximately 250 m from a block of forest (Figure 6.5). The paca site was located 1 km from an edge and 70 m (with a 30 m river crossing) from a hog plum swamp forest. The four detections at this site occurred over a 19-day period. Paca home ranges are 2-3 ha in size (Beck–King et al. 1999), pointing to the possibility that paca can persist in *Raphia* for extended periods. The armadillo site was near a grassland (<100 m) and forest (300 m). Though this species is known to use grasslands and human inhabited areas (Emmons and Feer 1997), it was never detected in grasslands in the study. Detections in *Raphia* (4%) were quite low compared to grey teak (60%), forest (30%) and oil palm (12%). The white-tailed deer was only detected once at a site 50 m from grasslands in a mixed *Raphia*, forest, and grassland area. A grassland site was the only other site detecting this species.

Other species detected in the landscape but not in *Raphia* are the white-lipped peccary (*Tayassu pecari)*, Baird's tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), puma (*Puma concolor*), red brocket deer (*Mazama temama*), tayra (*Eira barbara*), greater grison (*Galictis vittata*), coyote (*Canis latrans*), mantled howler monkey (*Alouatta palliata*), and Neotropical river otter (*Lontra longicaudis*).

The white-lipped peccary, jaguar, and Baird's tapir are of particular interest due to their high conservation status. The white-lipped peccary was only detected in a subset of cameras at Sirena Research Station in Corcovado National Park (CNP), but not in any part of the corridor sampled during this study. This species has been documented using *Raphia* seasonally (October–January) in nearby CNP (Carrillo et al. 2002), but based on interviews is only known to occasionally migrate into the western end of the study area where large *Raphia* stands are absent. Baird's tapir was detected in the corridor, about 10 km from the nearest *Raphia*. Tapir reportedly use *Raphia* in CNP

during the dry season, when palm fruits are falling (Wilson 1983, Naranjo 2009), and in Nicaragua (Jordan et al. 2010). The jaguar was reported by farmers living on the edge of *Raphia* to use this habitat but was not detected at any of the *Raphia* cameras. One farmer on a property bordered by an extensive *Raphia* stand and forest with a small area of pastureland provided a detailed report of sighting two jaguars passing through *Raphia* abutting his property. His story was supported by a jaguar detection on one of the study cameras placed in his pasture.

The other species (1) had low detection rates in the overall study, being detected at three or fewer cameras (greater grison, coyote, howler monkey and otter) (2) are largely arboreal (howler monkey) and/or (3) had a strong preference for forest habitats in this study (puma, tayra and red brocket deer).

Figure 6.3 Photos of four of the thirteen large mammal species detected by camera traps in *R. taedigera* stands on the Osa Peninsula, Costa Rica. Clockwise from top left: white-faced capuchin monkeys (*Cebus capucinus*), a paca (*Cuniculus paca*), collared peccaries (*Pecari tajacu*), and a nine-banded armadillo (*Dasypus novemcinctus*).

Table 6.1. Mammal and bird species detected in Raphia taedigera dominated landscapes on the Osa Peninsula, Costa Rica.

Common Name	Scientific Name	No. of times detected[1]	No. of sites	Detections / 100 trap days	% of cameras detecting (n=26)
Large Mammals					
White-nosed coati	*Nasua narica*	82	21	10.9	.81
Raccoon	*Procyon spp.*	77	15	10.2	.58
Collared peccary	*Pecari tajacu*	30	11	4.0	.42
White-faced capuchin	*Cebus capucinus*	13	8	1.7	.31
Ocelot	*Leopardus pardalis*	13	6	1.7	.23
Northern tamandua	*Tamandua mexicana*	12	8	1.5	.31
Central American agouti	*Dasyprocta punctata*	7	2	0.9	.08
Spotted paca	*Cuniculus paca*	4	1	0.5	.04
Jaguarundi	*Puma yagouaroundi*	4	3	0.5	.12
Striped hog-nosed skunk	*Conepatus semistriatus*	3	2	0.4	.08
Margay	*Leopardus wiedii*	1	1	0.1	.04
Nine-banded armadillo	*Dasypus novemcinctus*	1	1	0.1	.04
White-tailed deer	*Odocoileus virginianus*	1	1	0.1	.04
Small Mammals					
Gray four-eyed opossum[2]	*Philander opossum*	76	15	10.1	58
Mice and rats	Muridae	18	10	2.4	.38
Squirrels	Sciuridae	3	1	0.4	.04
Birds					
Grey-necked wood rail[3]	*Aramides cajaneus*	79	15	10.5	.58
Doves and pigeons	Columbidae	14	5	1.9	.19
White ibis[4]	*Eudocimus albus*	13	4	1.7	.15
Great egret[4]	*Ardea alba*	7	1	0.9	.04
Snowy egret[4]	*Egretta thula*	5	1	0.7	.04
Little blue heron[4]	*Egretta caerulea*	4	1	0.5	.04
Bare-throated Tiger Heron	*Tigrisoma mexicanum*	1	1	0.1	.04
Agami heron	*Agamia agami*	1	1	0.1	.04
Green heron	*Butorides virescens*	1	1	0.1	.04
Wood stork	*Mycteria americana*	1	1	0.1	.04

[1] A detection was considered independent of a prior detection of the same species if it occurred ≥ 30 min after the completion of a previous photo series.
[2] Of these detections, 32 were confirmed *P. opossum*. The remainder are likely this species.
[3] All except three detections were confirmed *A. caianeus*, the remainder are likely this species.
[4] One of the detections for each of these species was not confirmed but considered likely to be the species listed.

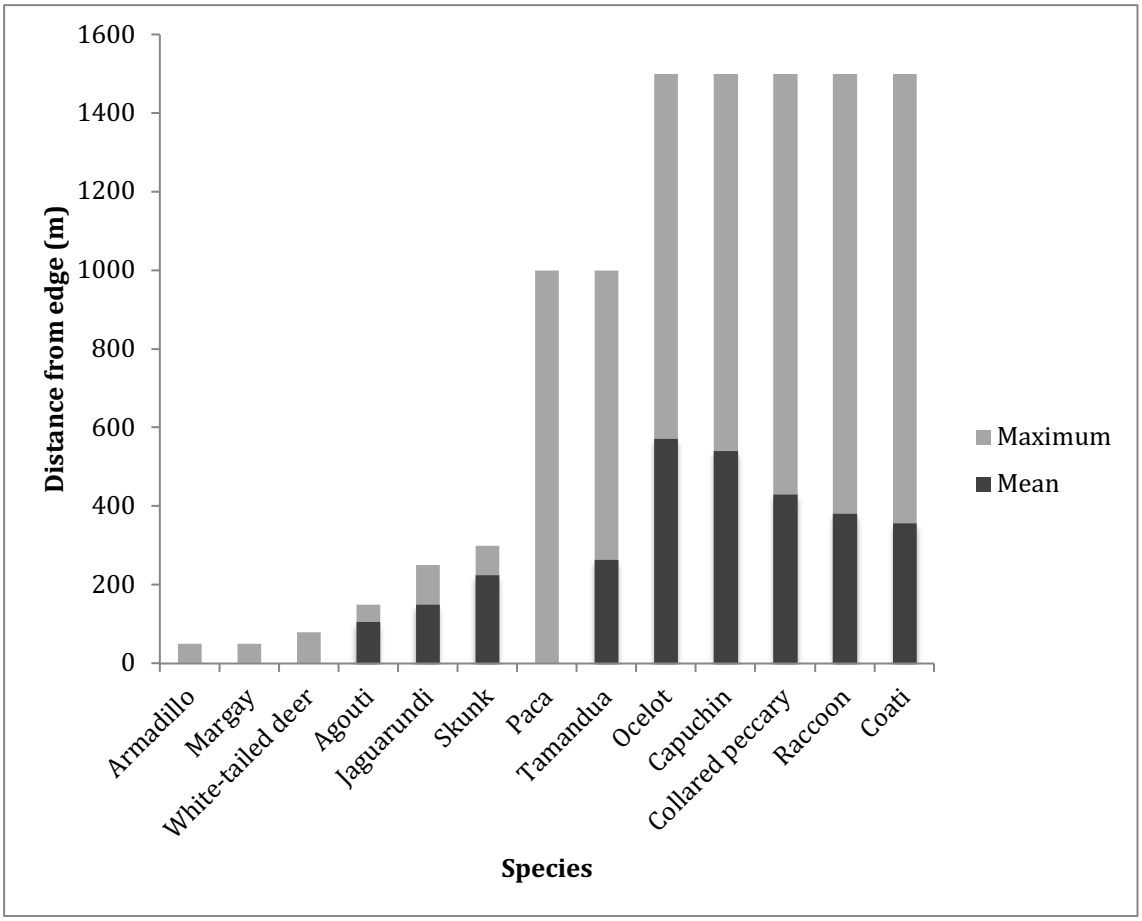

Figure 6.4 Distance large mammals traveled into *Raphia taedigera* stands on the Osa Peninsula, Costa Rica. The graph displays the maximum and mean (where multiple detections occurred) distance from the edge of a *R. taedigera* stand that each large mammal species was detected by camera trap within *R. taedigera* stands. Total sample size was 248 detections. Sample size for each species is listed above in Table 6.1.

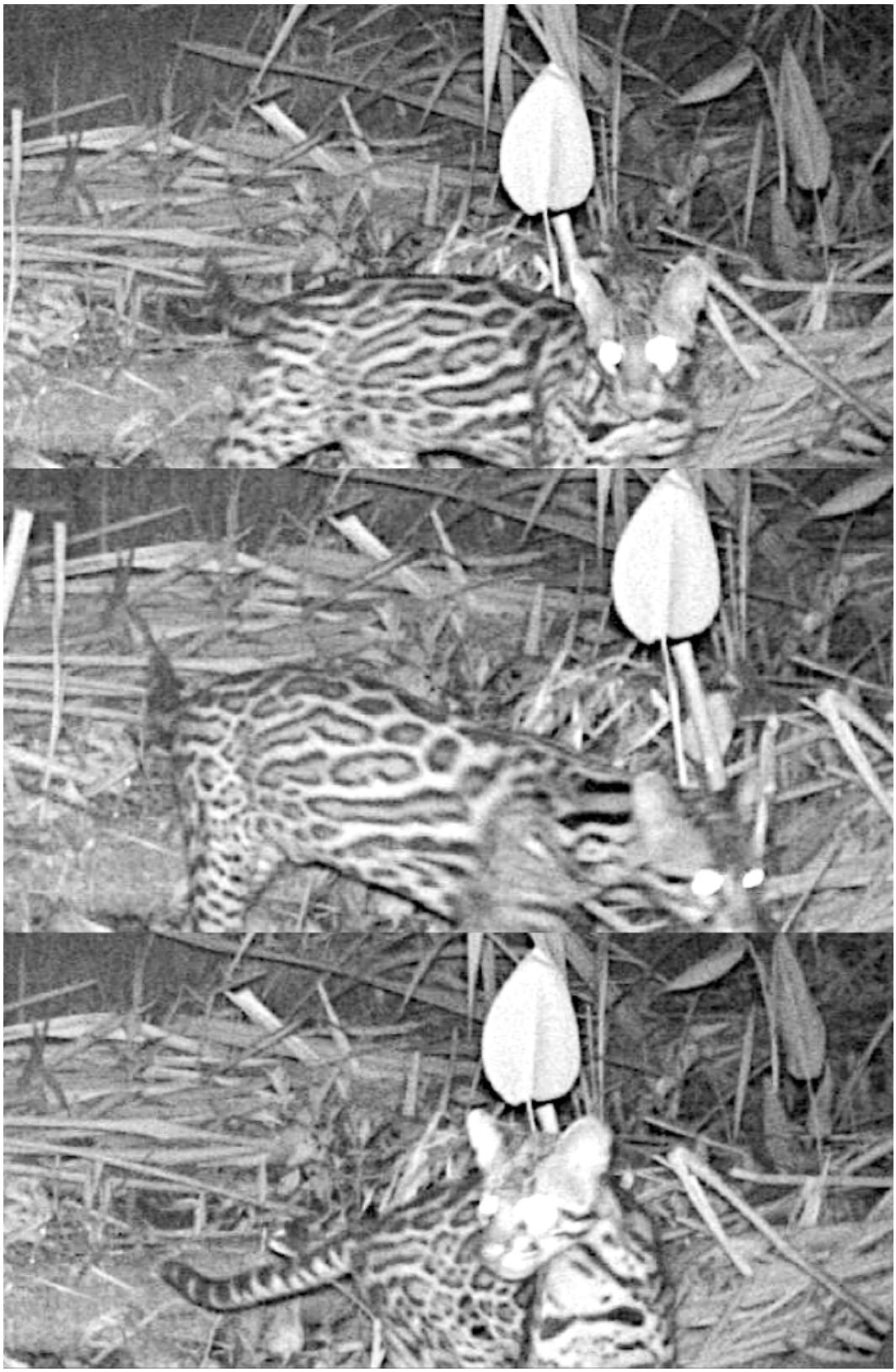

Figure 6.5 A series of photos of a margay (*Leopardus wiedii*) detected in a *Raphia taedigera* stand, approximately 250m from natural lowland forest, on the Osa Peninsula, Costa Rica.

Conclusion

To conclude, the *Raphia* forests provide useful habitat and a connectivity function in the Osa Biological Corridor for the coati, raccoon, collared peccary, white-faced capuchin, ocelot, tamandua and paca. It may also provide habitat and connectivity for the jaguarundi, agouti, margay and striped hog-nosed skunk, though detections were infrequent and these species remained near *Raphia* edges. Detection probabilities were low study-wide for many species, which may account for the low number of detections in *Raphia,* rather than an aversion to this habitat. Based on data from other studies and my camera and interview data, the tapir and white-lipped peccary do use *Raphia* but are unlikely present in *Raphia* stands in the study area due to hunting and habitat fragmentation. Finally, based on interview data, a detection adjacent to *Raphia*, and the high number of collared peccary detections (a jaguar prey species—Polisar et al. 2003, Carrillo et al. 2009), it is likely that jaguar will use *Raphia*, making it an important habitat to maintain connectivity across the Osa Biological Corridor. *Raphia* is likely to provide a similar habitat and connectivity function for large mammals in other Central and South American landscapes.

Acknowledgements

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Chapter 7 A comparison of rapid assessment methods for determining large mammal habitat use and distribution

This chapter is based upon a paper in preparation:

Yaap, B [a]**,** G. Paoli [b], H. Watson [c] and W. F. Laurance [a]. In Prep. A comparison of rapid assessment methods for determining large mammal habitat use and distribution. Journal to be determined.

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Statement of contribution of others:

Yaap was the lead author and lead researcher (study design, field data collection, data analysis and interpretation). Watson played a major role in field data collection and data entry. Expert interview data was collected by Yaap and Watson with Andrea Johnson translating. Camera trap deployment and community interviews were conducted by Yaap, Watson, Eduardo Nieto, Luis Fernando Quintero Gomez, Clara Vignolo and Andrea Johnson. Laurance and Paoli provided guidance on study design and analysis. Mason Campbell, Paoli and Laurance reviewed and provided edits to this chapter.

Abstract

High Conservation Value (HCV) mammal surveys rely heavily on rapid assessment techniques to survey proposed development areas. The time allotted for field surveys is usually short (1-4 weeks for an area of up to 50,000 ha), often too short to confirm the presence of rare or elusive species or taxa present in low densities. HCV mammal surveys therefore often use a combination of interviews, limited track and sign surveys, occasional camera traps, land cover, and the spatial arrangement of remaining natural areas to identify probable species presence and guide decision making for mammal conservation. To determine the reliability of interview data for identifying species presence and distribution in the landscape, I compare for twelve species the effectiveness of community and expert interview data with confirmed species detections (camera detections, direct sightings and indirect detections recorded while setting cameras). The comparison highlights the usefulness of interview data as a form of rapid assessment in HCV studies to complete a species inventory and gain insight into species distributions. No one method stood out as consistently superior for all species. Rather, all three methods were informative in different ways, together providing a more comprehensive understanding of localized species distribution than any single method. Some methods appear likely to provide better results for specific species and could enable reduced survey effort. The lack of single superior method highlights the need for a multi-faceted strategy to undertake rapid mammal surveys and inform specific approaches for doing so, especially mammal surveys for HCV assessments. Recommendation are provided for employing each method for rapid HCV mammal assessments.

Introduction

Many development activities require a rapid survey of the biological resources within the proposed development area and its immediate surrounds. High Conservation Value (HCV) mammal surveys rely heavily on rapid assessment techniques to survey proposed development areas (HCVRN 2013, Stewart et al. 2007, Stewart et al. 2008). The goal of such surveys is to create a species inventory, identify the presence of threatened species, and subsequently delineate priority areas for conservation. Where

time allows, species abundance and diversity are also sometimes measured. Such rapid surveys employ a variety of techniques, including track and sign surveys, interviews, and camera trapping. The time allotted for field surveys is usually short (1-4 weeks for an area of up to 50,000 ha), too short to confirm the presence of most rare or elusive species or taxa present in low densities (O'Connell et al. 2011).The short time allotted for field data collection can even be inadequate to undertake established rapid assessment methods for surveying terrestrial mammals that rely heavily on systematic line transects (e.g., Benchimol 2016). Line transect methods often return few detections for rare mammal species (Plumptre 2000), species which are often of conservation concern (listed as threatened by the International Union for Nature Conservation (IUCN) Red List of Threatened Species) (Yu and Dobson 2000). HCV mammal surveys therefore often use a combination of interviews, limited track and sign surveys, camera traps, land cover surrogates, and the spatial arrangement of remaining natural areas to identify probable species presence and thereby guide decision making for mammal conservation.

Numerous studies have shown that camera traps are an effective tool for surveying medium and large mammals, especially rare, elusive and/or nocturnal species (O'Connell et al. 2011, Kelly 2008). Yet, detection of a comprehensive list of mammal species using camera trap data requires extensive survey effort (e.g., 1,000 trap days; Carbone et al. 2001), exceeding the time frame available for HCV assessments. Interviews with local residents, especially hunters, and land managers are also viewed as valuable input for conducting species inventories and identifying species distributions (e.g., Zeller et al. 2011, Can and Togan 2009), but caution must be shown given limitations and risk of potential errors (e.g., misidentification) (Can and Togan 2009, Hellier et al. 1999), especially with rare species (McKelvey et al. 2008).

In this chapter I assess expert and local peoples' knowledge of species distributions and compare these to each other and comprehensive camera trap survey data. I aim to identify the applicability of interview data for HCV rapid assessments of large mammals. To achieve this aim, I compare community and expert interview data with confirmed species detections (camera detections, direct sightings and sign detections collected while setting cameras) to assess the reliability of interview data and camera

traps for identifying species presence and distribution on Costa Rica's Osa Peninsula. Results are intended to help inform survey design and implementation HCV rapid assessments of large mammals.

Methods

Study Area

The study area is an approximately 740 km^2 area located on the northern part of Costa Rica's Osa Peninsula (Figures 1.2 and 5.1). It is part of a landscape linkage located between reserves or natural areas (Category 1 in Chapter 2), described in detail in the Methods section of Chapter 5.

Data Collection

Twelve mammal species of interest were selected for study based on conservation status (listed as threatened by IUCN, i.e., Endangered or Vulnerable), unknown presence in the study area, taxonomic group (e.g., primates) and/or low probability of detection by cameras traps. On this basis, I selected the collared-peccary, white-lipped peccary, jaguar, puma, red brocket deer, white-tailed deer, tapir, coyote and four primates known to the peninsula – howler monkey, squirrel monkey, spider monkey, and capuchin (Table 7.1).

Interviews were conducted opportunistically with residents in the study area (n = 42 (mean), range = 14; not all interview respondents were interviewed for every species) while setting cameras. Many of the camera sites (see Chapter 5 for detailed methods) were on private lands which created an opportunity to interview land owners or caretakers whilst getting permission to deploy cameras on their properties. These interactions with land owners and care takers accounted for the vast majority of interviews. Where possible, I recorded the respondent's name, length of time living in the area, occupation, the stated presence/absence of each of the targeted mammal species, as well as additional information on which species in the area are hunted (refer to Appendix G for data sheet). If a species was reported present I requested further information on its habitat, last sighting and how frequently it was present in the area. The extent of respondents' geographic area of knowledge varied

considerably between respondents depending on their job and day-to-day activities (e.g., cattle farmer, oil palm worker or farmer, house wife), hobbies (such as hunting), and the location of their home (e.g., near a town, or in a location requiring extensive journeys by river or horseback to reach their farm). For example, interview responses could reflect an area as small as 2 km^2 or as large as 10 km^2. During the interviews, the locale of species identified as "present" was confirmed by asking the respondent for specific geographic locations based on local landmarks. In instances where respondents identified a species as present in a distant area, the species was not marked as present for the interview locale or the distant location. Interview length and the level of detail of the questions posed (and responses) varied depending on time available and a respondent's interest level in engaging in an extended interview. Hereafter these interviews will be referred to as "community interviews".

A local expert, the Golfo Dulce Forest Reserve Manager for Costa Rica's Área de Conservación Osa (ACOSA) - Sistema Nacional de Areas de Conservacion (SINAC) (Juan Jose Jimenez Espinoza), was also interviewed (29th of May 2013) about the presence and distribution of the target species. Drawing on his knowledge of the study area from working with researchers and land owners on the Osa Peninsula, he was asked to identify locations where he expected each species to be present/absent/uncertain, sketching out his responses on a map of the study area during the interview. He also provided additional information on why he expected his suggested species distributions.

Camera trapping data collection methods are described in the Methods section of Chapter 5.

Data Analysis

To compare species prevalence in the landscape (as shown by cameras) with the likelihood of identifying a species as "present" using community interviews, I plotted the percentage of camera sites where a species was detected versus the percentage of interview respondents identifying the same species as "present" in their local area. For each target species, I used ArcGIS to create a map for visual comparison of (a) interview data (interviewee responses – "present" or "absent") and (b) confirmed

species records (sites where species were confirmed present by camera or direct or indirect detection by my survey team) with (c) species distribution maps created from occupancy models derived from camera data (refer to Chapter 5 for methods). For species with insufficient detection data to create a distribution map as a base layer, I overlaid confirmed species detections (camera, track, sighting or calls) and interview data with known habitat associations of each species (as determined by literature review). A qualitative comparison of results for each method (community interviews, expert interview, and camera trapping) are discussed for each species, along with a conclusion as to the usefulness and accuracy of each survey method which is summarized and ranked on a scale of 1-3. Scoring for community and expert interviews were based on the degree of alignment with camera trap survey data and usefulness of information not provided by cameras (Table 7.1).

Table 7.1 Scoring system used to rate the efficacy of each survey method on the Osa Peninsula, Costa Rica.

Score	Community and expert interviews	Camera trap survey
1	Not well aligned with camera data, or extensive disagreement about the species presence in community interviews.	Very slow detection rate (TFD >500 trap days), or not detected, but species likely present.
2	Relatively well aligned with camera data, yet some clear misalignment or knowledge gaps; Information provided insightful, but not essential, addition information to camera data.	Medium detection rate (TFD >250 trap days).
3	Well aligned with camera data; information provides important additional information about species distribution; and/or provides the best information available of the three methods.	Quickly detected (average TFD <250 trap days of sampling in known habitat); was the most reliable method of identification; and/or provided important location information missed by interviews.

The number of trap days required to detect each species (time to first detection – TFD) was also compared collectively (over the course of the entire study) and per sampling cycle. I defined a sampling cycle as one complete round of setting all cameras for the 28-day minimum period. There were four such cycles across the study period. Only cameras placed in a species' preferred habitat were included in the calculations. Preferred habitat was identified by camera data from this study and literature review, and was identified as forest for most species. The focus on forest camera data was also with the intention of reflecting camera placement in an HCV rapid assessment

scenario, which is most likely to focus on sampling remaining forest in or surrounding a proposed development site. The collective TFD metric was insightful for species that were rarely detected or not detected until one of the latter sampling cycles, often revealing a high overall sample effort to detect the species. Averaging the per cycle TFD was most informative for species that were more frequently detected, providing an average sampling effort to detect a species. Scoring for camera trap survey data was also done on a scale of 1-3, but based on the time until first detection (TFD) (i.e., number of trap days to detect a species) and importance in relation to interview data (Table 7.1). Scoring for camera trap efficacy was based on a collective total of sampling says for a sampling cycle; for example, 10 cameras set for 5 nights equals 50 trap days.

Table 7.2 Mammal species surveyed using interview methods during the study on the Osa Peninsula, Costa Rica. Species information includes their International Union for Conservation of Nature (IUCN) Red List conservation status and data available from each data collection method used during the study period.

Common Name	Scientific Name[#]	IUCN	Community interview	Expert interview	Camera trap	Signs/ sightings/ calls
Collared peccary	*Pecari tajacu*	LC	x	x	x	None
White-lipped peccary*	*Tayassu pecari*	VU	x	x	Sirena only	None
Jaguar	*Panthera onca*	NT	x	x	x	x
Puma	*Puma concolor*	LC	x	x	x	x
Red brocket	*Mazama temama*	DD	x	x	x	None
White-tailed deer	*Odocoileus virginianus*	LC	x	None	x	None
Tapir	*Tapirus bairdii*	EN	x	x	x	x
Coyote	*Canis latrans*	LC	x	x	x	None
White-faced capuchin	*Cebus capucinus*	LC	x	x	x	x
Geoffroy's spider monkey	*Ateles geoffroyi*	EN	x	x	None	x
Central American squirrel monkey	*Saimiri oerstedii*	VU	x	x	None	x
Mantled howler monkey	*Alouatta palliata*	LC	x	x	x	x

* Only detected at Sirena Research Station in Corcovado National Park, not detected in the study area.
[#] DD = Data deficient, EN = Endangered, LC = Least Concern, NT = Near threatened, VU = Vulnerable.

Results & Discussion

Species prevalence

There was a positive correlation between community interview respondents reporting of species presence in the study area and their increased prevalence as determined by camera trapping (Figure 7.1). The white-lipped peccary was one exception; it was not detected by camera trapping in the study area, but was identified as present by 32% of

respondents. There is a history of occasional migrations of this species in the study area (Jimenez 2012, Altrichter and Almeida 2002) which could account for the discrepancy. Furthermore, more than 60% of respondents reported jaguars as present, but the species was only detected at five sites (Figure 7.1). The disparity in interview responses and camera data is likely a reflection of camera placement and low density of this species as jaguars have large home ranges and exist at low densities (Salom-Pérez et al. 2007) and cameras in this study were not set to specifically target jaguars which is known to influence detection probability (Harmsen et al. 2010, Sollmann et al. 2011). The disparity in interview responses and camera data is therefore likely a reflection of camera placement and low density of this species. Residents' awareness of jaguar presence may also have been inflated for several additional reasons: jaguar pugmarks are distinct (though able to be confused with pumas), there is an ongoing jaguar research project in the area that has likely alerted residents to this species' presence, and hunters and residents report their dogs being eaten by jaguars (stories that travel well in conversation). It is therefore not surprising the jaguar was frequently identified as present whilst prevalence, as determined by cameras, was low.

Primates in the study area were difficult to detect with cameras due to their largely arboreal nature and the fact that cameras were set close to the ground during the study so as to target terrestrial species. The white-faced capuchin was an exception. Detected at 10% of cameras, it is often terrestrial, uses a variety of habitats and is readily observed by humans (Wainwright 2007). Considering these factors, it is intuitive that interview data showed a much higher proportional prevalence of primates than cameras. Interview data for primates also followed the expected pattern of rarity based on their habitat needs and conservation status. For example, since Geoffroy's spider monkeys (IUCN: Endangered) and Central American squirrel monkeys (IUCN: Vulnerable) are both threatened species, with more restrictive habitat needs than white-face capuchin and mantled howler monkeys, I expected spider monkeys and squirrel monkeys to be less abundant in the study area which was reflected in the interview data (Figure 7.1).

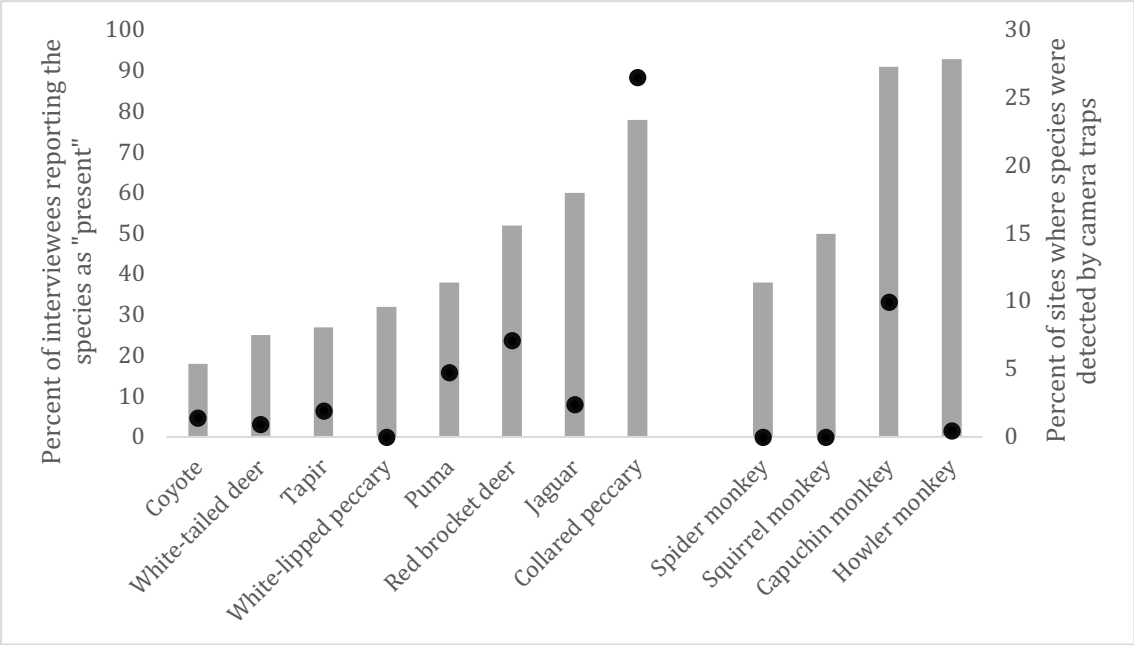


Figure 7.1 Percentage of respondents reporting the target mammal species "present" in the study area (bars) compared to species prevalence as identified by camera traps (the percent of camera sites where the species was detected) (points) on Costa Rica's Osa Peninsula.

Species distribution

The reliability of an expert interview and community interviews for surveying the presence and distribution of each species as compared to camera trap data is analyzed and discussed in the sections below and summarized in table format in Table 7.2.

Peccaries

Camera Trap Data

My camera trap survey confirmed that the collared peccary is present across the entire study area, but more prevalent in the eastern end which adjoins and comprises part of Piedras Blancas National Park (Figure 7.2). As previously determined by occupancy models using camera trap data (Chapter 5), collared peccaries showed aversion to grassland, mangrove and oil palm habitats and roads, a strong preference for forest, and some intermediate level usage of *Raphia*. Camera traps readily detected collared peccaries in the forest component of the study area, taking an average of 53 trap days

(in the four sampling cycles) to first detection, 230 trap days to first detection in study (Table 7.3).

I did not detect white-lipped peccaries in the study area. During a one-month long experimental camera trapping exercise at the Sirena Research Station (SRS) in Corcovado National Park (CNP), located south-west of the study area (Figure 5.1), I tested species responses to the scent lure I used at each camera station in the overall study (refer to methods in Chapter 5) by setting six cameras in pairs of two (one with scent lure and one without). In this experiment I detected both species of peccary at all six camera sites. As such, it is unlikely that the scent lure I used during my camera trap sampling of the study area influenced the absence of detections of the white-lipped peccary in the study area. Further, during the SRS experiment the white-lipped peccary was readily detected, taking thirty trap days until first detection and being detected by at least one of the six cameras on 50% of all trap days.

Migrations of white-lipped peccary take place in response to fruit availability (Carrillo et al. 2002). The species migrates out of Corcovado NP during the late wet season (Altrichter and Almeida 2002) (wet season: May - November) in response to increased fruit availability in surrounding dryland forest and subsequently returns to the park October - January when fruit availability in dryland forests is at its lowest (October - January) (Carrillo et al. 2002). If the white-lipped peccary is indeed present in the study area, it is highly likely that it is via occasional, seasonal migration during periods when I was not sampling for this study.

Interview Data

Juan Jose Jimenez Espinoza, the local environmental expert, correctly predicted that the collared peccary would be prevalent in the east of the study area (Figure 7.2). However, he was uncertain about this species' presence in the west of the study area where he predicted it may be displaced by the white-lipped peccary (Figure 7.3). His knowledge of white-lipped peccary presence in the west of the study area was based on an incident that took place around 2009 when a herd of peccary became resident behind the school in Rancho Quemado (in the west of the study area). Approximately 70 individuals were culled by local community members despite the Ministry of

Environment and Energy's (MINAE) efforts to protect the herd – community members were frustrated at the perception of MINAE prioritizing the safety of the peccaries over human residents. Community interviews corroborated this account. While, his predictions aligned well with the camera trap data in identifying a prevalence of the collared peccary in the east, camera traps were also able to confirm its presence in the west (Figure 7.2). His knowledge of white-lipped peccary history in the area provided valuable additional information to the camera survey.

The vast majority of community interview respondents reported collared peccary "present" across the study area, including in the west, which my camera data confirmed. Most community interview respondents said the white-lipped peccary was absent in the study area, with respondents noting that it still exists in forest areas in Corcovado and deep in PBNP. However, it is questionable whether the white-lipped peccary is currently present in PBNP as the IUCN Red List has the remaining distribution in CNP alone (Keuroghlian et al. 2013, though see Wainwright 2007 and Landmann et al. 2008). Further, judging by how readily the species was detected by my cameras at Sirena Research Station in CNP, it is likely the species was not present in the study area during the sampling period. The apparent absence of this species in the study area and PBNP is likely a result of hunting and habitat loss (Carrillo et al. 2000, Altrichter and Almeida 2002, Carrillo et al. 2009) as high levels of hunting pressure in the area have been documented and this species requires large areas (Keuroghlian et al. 2013) and undertakes seasonal migrations to exploit food resources (Carrillo et al. 2002).

Summary

When present, both peccary species are readily detected by camera traps. This survey method effectively identified the presence and abundance of the collared peccary and likely absence of the white-lipped peccary. However, interview data from the expert provided information about historic seasonal migrations into the study area that would not have been captured during my extensive five-months of camera sampling. Meanwhile, community interviews accurately identified the distribution of the collared peccary and the rarity of white-lipped peccary. However, community respondents

misidentified the white-lipped peccary as present in PBNP and the Gulfo Dulce Forest Reserve (they are likely now extirpated by hunting and habitat loss) due to historic presence. In conclusion, camera trapping and community interview data were the most effective for identifying the distribution of the collared peccary, while the camera trapping and the expert interview data were most informative for understanding the absence of the white-lipped peccary.

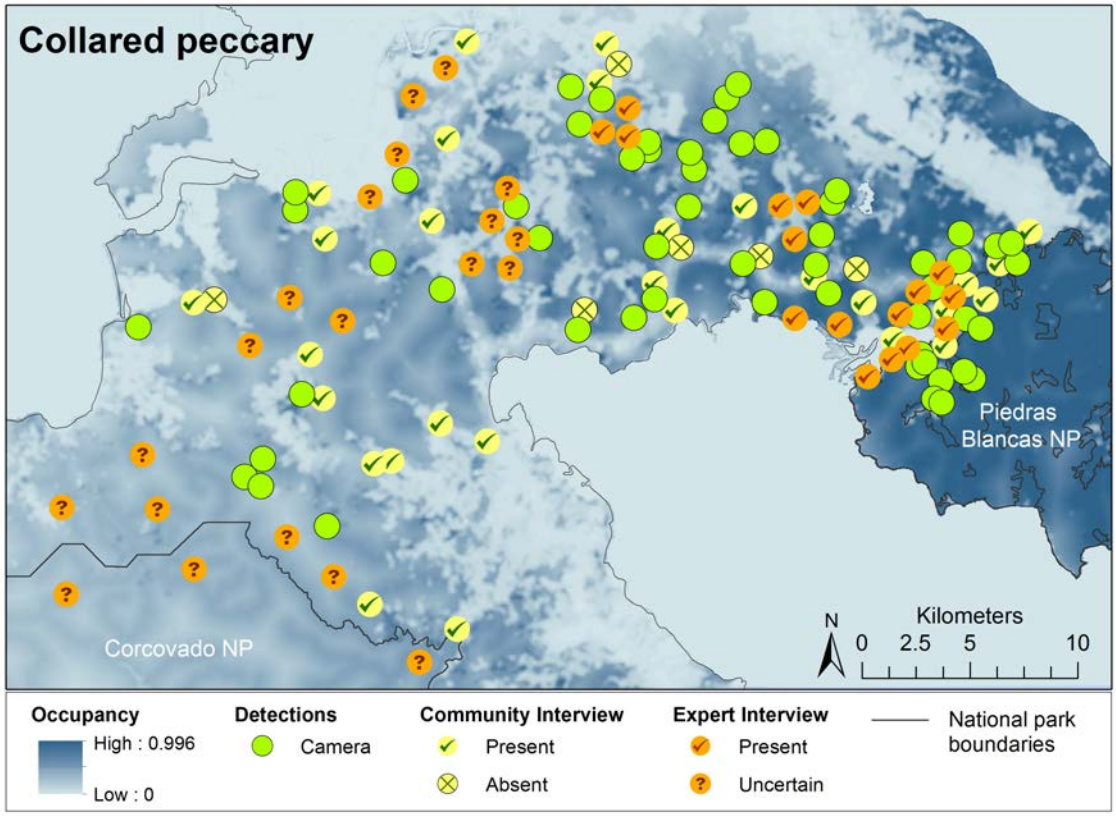


Figure 7.2 Map displaying collared peccary (Pecari tajacu) distribution using multiple sampling methods (camera trap, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

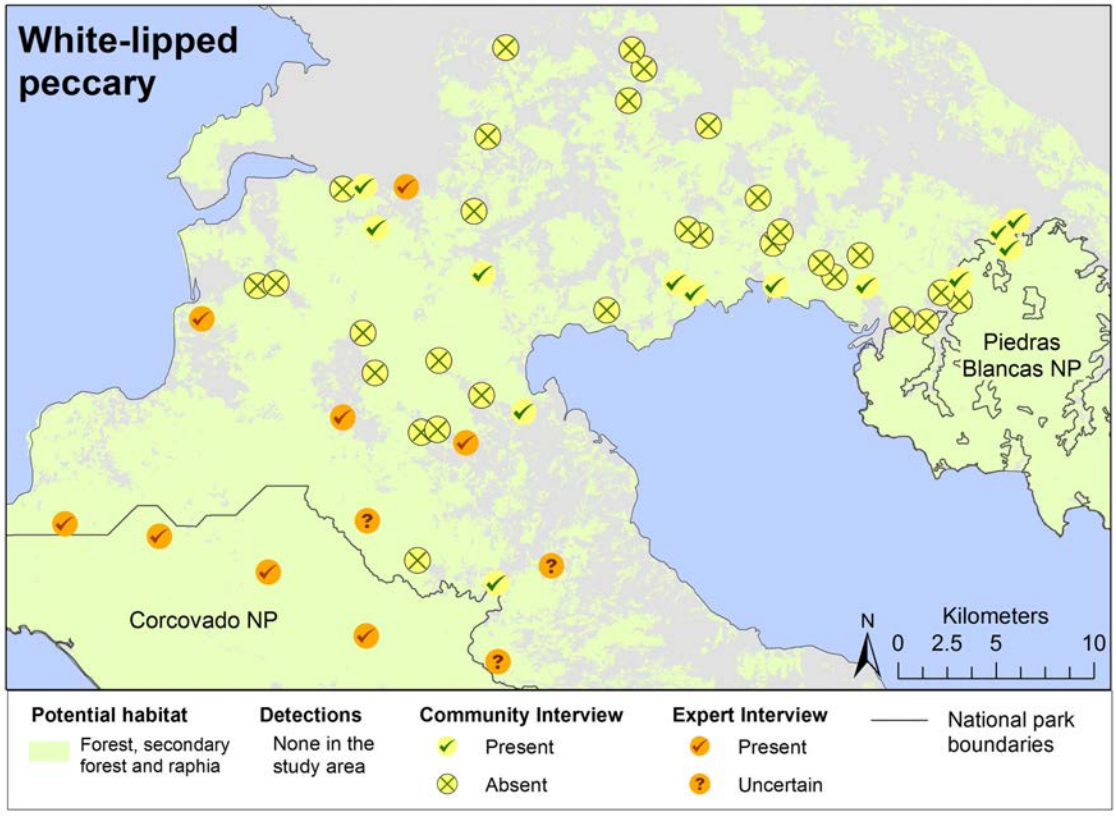


Figure 7.3 Map displaying white-lipped peccary (Tayassu pecari) distribution using multiple sampling methods (camera trap, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review.

Large cats

Camera Trap Data

Using the camera trap data I confirmed that both jaguar and puma are present in the study area (Figures 7.4 and 7.5). Jaguars were detected in the middle and eastern parts of the study area, including one detection in an area dominated by *Raphia* (most northern camera detection point in Figure 7.4). All other detections were in forest in the eastern part of the study area, closest to CNP. Pumas were only detected in forested habitats, predominantly at sites closer to CNP and PBNP (Figure 7.5).

For camera traps set in forest, it took 1,056 trap days to obtain my first jaguar detection, and 488 days to detect my first puma (Table 7.3). In the four trapping cycles, it took an average of 185 days to detect a jaguar (in the three cycles when it

was detected) and 389 days to detect a puma (detected in all four cycles). The time to first detection in this study emphasize the relatively high number of trap days necessary to detect these species with camera traps and is likely attributed to low densities and large home ranges of these two species.

Interview Data

The expert was confident that jaguars were present across the study area and deep in CNP and PBNP, but uncertain about the species' presence in certain areas, such as Sabalo and the Guaymi Reserve (Figure 7.4). He stated that jaguar will cross any habitat, including *Raphia*, grassland and oil palm plantations, to obtain prey (mostly peccary). He also discussed their predation on sea turtles along the coast. Community interviews largely reported the jaguar as present across the study area, though absent in the north and in costal locations where forest is absent.

The expert was uncertain of puma distribution in the study area due to a lack of reported sightings. However, he thought the species was possibly present in the southwestern part of the study area, near the Guaymi Reserve. He also thought puma presence may be confused with that of jaguars by land owners. Corroborating this opinion, community interview respondents mostly reported the puma as absent in the study area (Figure 7.4).

Summary

Jaguar distribution findings from camera data aligned well with expert and community interview data. However, it is possible that jaguar presence is inflated in community interviews due to confusion with puma signs and word of mouth about its presence from researchers working on the peninsula. The camera traps did not confirm jaguar presence in the east of the study area, however this may be due to camera placement (cameras were not always set on trails likely to be used by jaguars) and theft (some cameras placed along prominent trails likely to be used by jaguars were stolen) because jaguar presence has been confirmed in the east of the study area by other camera trapping projects (Saladero Ecolodge 2017). Analogously, Landmann et al. (2008) deemed jaguars present in PBNP based on local expert (nature guides, park game wardens present, and local hunters) opinion, but conceded that the species had

not been detected by scientific researchers working in the area. To gain a better understanding of the jaguar population and distribution across the Osa Peninsula, a collaborative project is now underway, led by SINAC-ACOSA, to identify individual jaguars in the region from the myriad of past and present camera trapping projects, including the present study. Early analyses show at least one individual has traversed the study area from east to west, detected both in the PBNP and the western portion of the study area.

Interestingly, the pumas were not identified as present in PBNP by Landmann et al. (2008) using interview data from experts and scientists nor through their research sampling, yet they were detected in the park by camera trap in 2015 (Saladero Ecolodge 2017). Community interview data results for puma presence in PBNP were mixed though on average the species largely deemed absent across the study area (Figure 7.5). Conversely, my cameras twice detected pumas across the Esquinas River from PNBP (Figure 7.5). Camera data was therefore essential in identifying the presence of the puma in the study area.

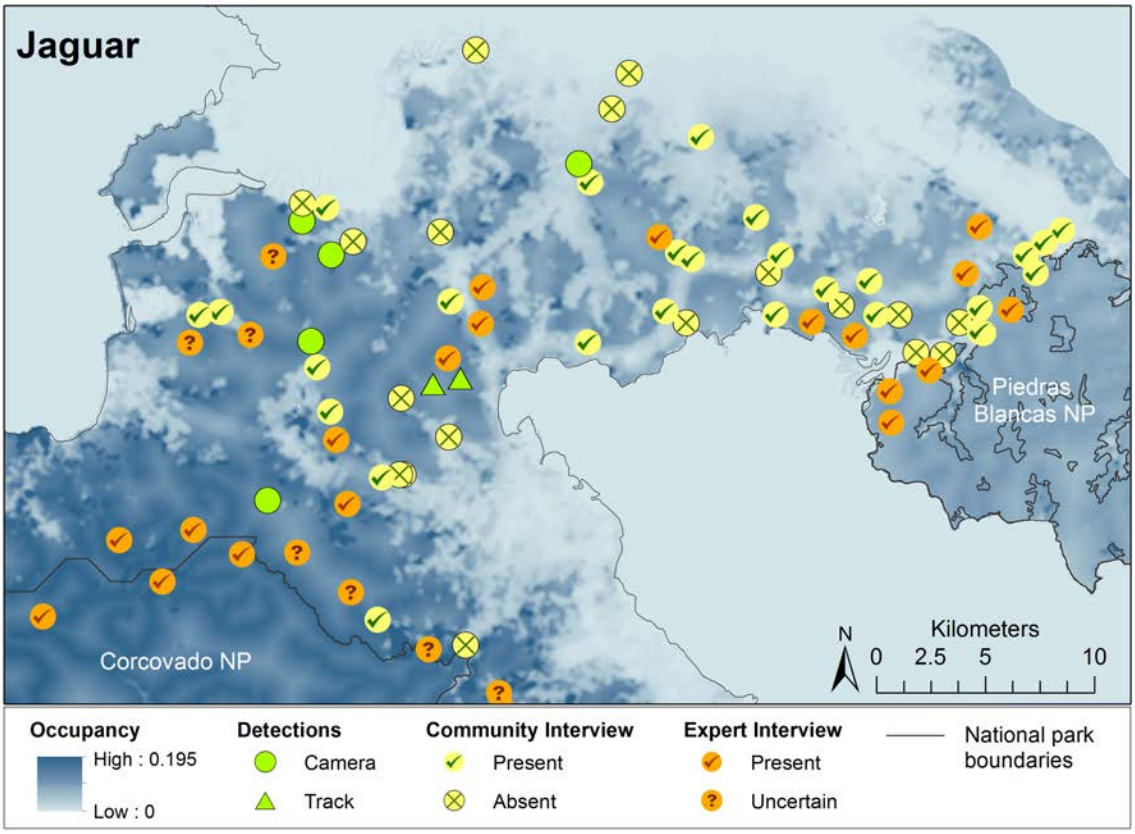


Figure 7.4 Map displaying jaguar (*Panthera onca*) distribution using multiple sampling methods (camera trap, tracks, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

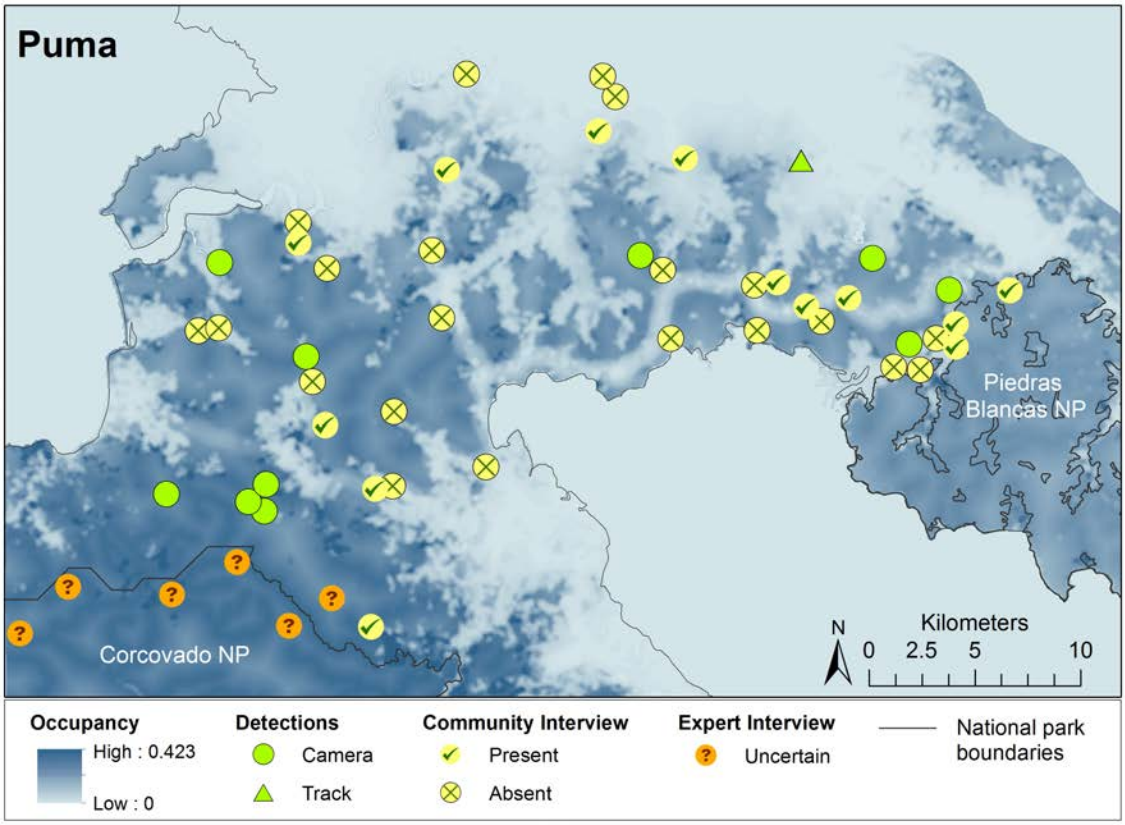


Figure 7.5 Map displaying puma (*Puma concolor*) distribution using multiple sampling methods (camera trap, tracks, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

Deer

Camera Trap Data

Red brocket deer were detected by camera traps at both ends of the study area, but infrequently (at one camera) in the center of the study area, where forest becomes patchy (Figure 7.6). This species of deer was detected relatively quickly at forest sites – 42 trap days to first detection in the overall study, and an average of 174 trap days to first detection across the four trapping cycles (Table 7.3). Red brocket deer were only detected by camera traps set in forest and melina (grey teak; *Gmelina arborea*) stands which aligns well with the species known habitat preference for forests and forest edge habitats (Wainwright 2007).

The white-tailed deer was only detected at a single camera in each of the grassland and *Raphia* habitat types (Figure 7.7). Both detections were in the northern part of the

study area where degraded lands (pasture lands and agriculture) dominate the landscape (Figure 7.7). The species was not quickly detected by camera trap – taking 593 trap days to detect in habitats where it was detected in this study (grassland and *Raphia*), and an average of 188 trap days to first detection across the two trapping cycles when it was detected (Table 7.3). The infrequent detections and slow detection rate was likely a result of the species' limited distribution in the study area.

Interview Data

The expert was uncertain of red brocket deer distribution across the north of the study area – areas where the species was not detected by cameras (Figure 7.6). He was not interviewed about white-tailed deer distribution.

Community interview respondents reported red brocket deer present in the north of the study area (Figure 7.7). The species was not detected by camera traps in this area and, if present, is likely to be present at very low densities based on the limited amount of forest habitat in this part of the study area. Community interview respondents accurately identified the presence of the white-tailed deer in the north of the study area (with all respondents in this area saying the species was present) and predominantly reported it as absent in the other parts of the study area (Figure 7.7).

Summary

Camera trapping survey data were effective in indicating low occupancy of red brocket deer in the north of the study area. They were especially useful in that community interview data contradicted this low occupancy finding, and the expert was uncertain of their presence. In fact, community interview data was conflicting with respondents living adjacent to each other having differing responses. For the white-tailed deer, camera and community interview survey data were well aligned in the northern part of the study area where the species was confirmed present by camera trap data. Interview respondents identified additional locations where the species was not detected by camera traps, but suitable habitat is present, lending to the possibility that the species is present in these areas, possibly in low densities, but was not detected by the camera trap survey.

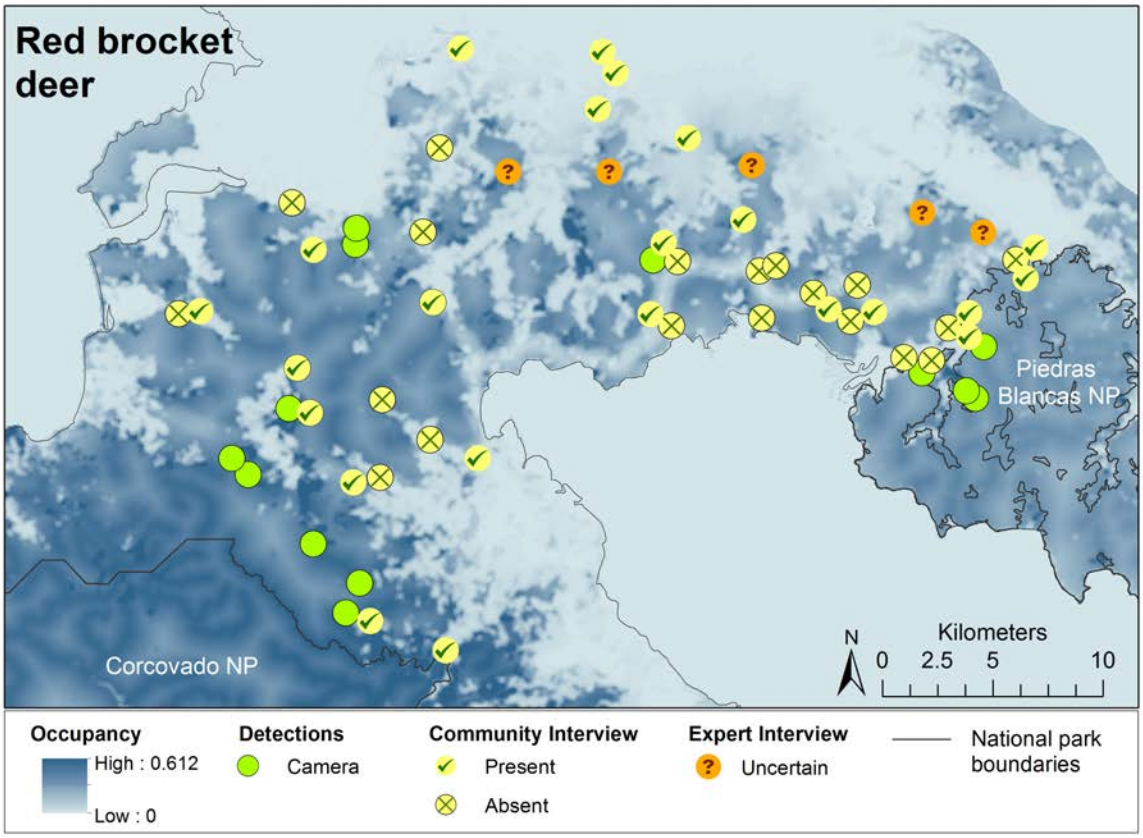


Figure 7.6 Map displaying red brocket (Mazama temama) distribution using multiple sampling methods (camera trap, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

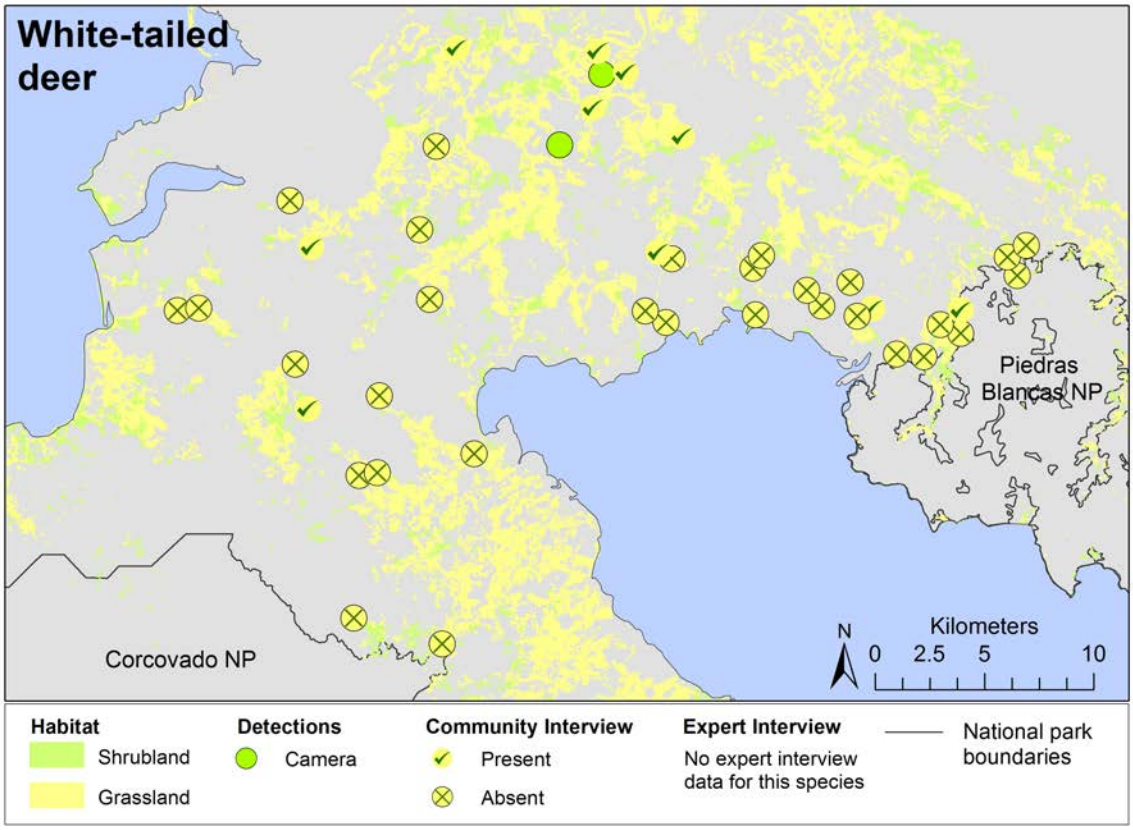


Figure 7.7 Map displaying white-tailed deer (*Odocoileus virginianus*) distribution using multiple sampling methods (camera trap, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review.

Tapir

Camera Trap and Other Detection Data

I identified tapirs in the eastern and western ends of the study area using camera trap surveys and tracks presence. Tapir detections were restricted to forested areas (Figure 7.8). An eco-lodge owner showed my survey team a tapir print cast from their property at one of my camera trap sites that was made a few months earlier. I included this record as a "track" detection (labelled "A" in Figure 7.8) for the site. This detection record was the only one in the southern strip of forest that follows the shore of the Gulfo Dulce (Figure 5.1); an area that is likely one of the most important areas of forest connectivity between CNP and PBNP for forest dependent species.

Interview Data

The expert-identified tapir locations aligned well with the camera trap survey data. These survey techniques were also complementary in that in a few areas where the expert was uncertain of tapir presence this uncertainty was clarified through camera detections (e.g., areas labelled “B” and “C” in Figure 7.8). The expert also shared informative background information on the historic distribution of the species. The last reported hunting of a tapir was in 2011 in the Los Planes area (in the far east of the study area, near Drake and the northern border of Corcovado NP) due to a tapir destroying a land owner’s bean field. There were also recent sightings of a tapir in BPNP wearing a radio collar. This individual is likely to have crossed the study area from CNP to PBNP as several tapirs had been radio collared as part of a tracking study in Corcovado NP, though park rangers were unable to personally confirm the observation.

Community interview data aligned well with findings of the camera trap survey (and associated track detections), though two discrepancies were identified. The camera trap survey confirmed tapir presence in an area where tapirs were thought absent by community interview respondents (labelled “B” in Figure 7.8) and a track was identified in an area where all but one respondent thought the species was absent (labelled “A” in Figure 7.8). Some respondent also identified tapirs as pests, destroying beans planted in their gardens.

Importantly, both community and expert interviews identified tapirs as present in one area that is likely of key importance for overall landscape connectivity where the species was not detected by camera traps (labelled “D” in Figure 7.8). The ability of each method to provide clarification and additional insight to other methods displays the overall complementarity of the approaches analysed and the importance of using multiple approaches to gain a more complete understanding of tapir distribution.

Summary

Interview and camera survey data draw into question east-west connectivity across the study area for tapirs. No camera trap detections occurred in the middle of the study area and interview respondents in the north of the study area stated that tapirs

are absent as did most respondents in the forested areas in the south (following the Gulfo Dulce coast line). The exception is in the area where a track cast was taken (as described above) and a couple of sites in the north of PBNP where community interview respondents and the local expert identified tapir as present (Figure 7.8). If tapirs are traversing the middle section of the study area it is likely to be occasional and via the remnant forest in the south.

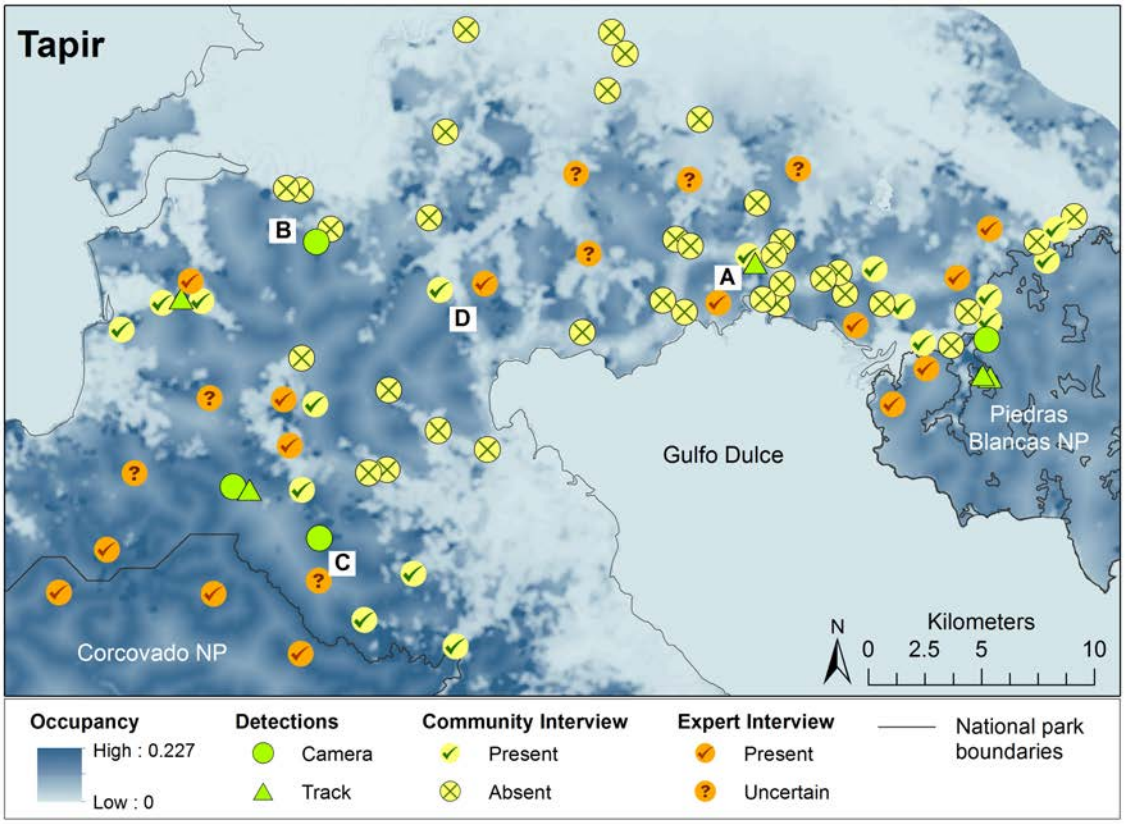


Figure 7.8 Map displaying Baird's tapir (*Tapirus bairdii*) distribution using multiple sampling methods (camera trap, track, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

Coyote

Camera Trap Data

Coyotes were detected at three camera trap sites during the study (Figure 7.9). In the northern region of the study area coyotes were detected twice in grassland, two days

apart in an area that is on the edge of a large expanse of degraded land. The other detection occurred in an oil palm plantation. All coyote detections occurred during a 20 day period in March and April, 2013. It took 555 days to detect the species since the commencement of the study, but only 54 days from the beginning of the survey cycle during which it was detected.

Interview Data

The local expert was uncertain of coyote presence on the Osa Peninsula but predicted it would be in degraded parts of the landscape if it was present. This agrees with my findings from the camera trap survey data and known habitat preferences of the coyote in Costa Rica (Wainwright 2007).

Community interviews mostly reported the species as absent in the landscape, but several respondents reported it present in areas near the camera trap sites which detected the species – showing a strong correlation between the community interview and camera trap data for this species. Respondents also reported coyotes as frequently present in the Sierpe area (northern part of the study area) and occasionally present in other areas along the PBNP boundary. Respondents identifying coyotes as present stated that the species has only arrived in the study area in recent years.

Summary

Camera trap surveying was effective in confirming coyote presence in the study area. This photographic evidence was vital given most community interviewees did not think the species was present in the south-central part of the study area which could lead to researchers questioning its presence. Further, expert interview data was not informative for this species, which is likely a reflection of what seems to be the recent arrival of the species on the Osa Peninsula. Finally, coyotes were only detected during one sample cycle potentially suggesting that the study area is only periodically used by this species.

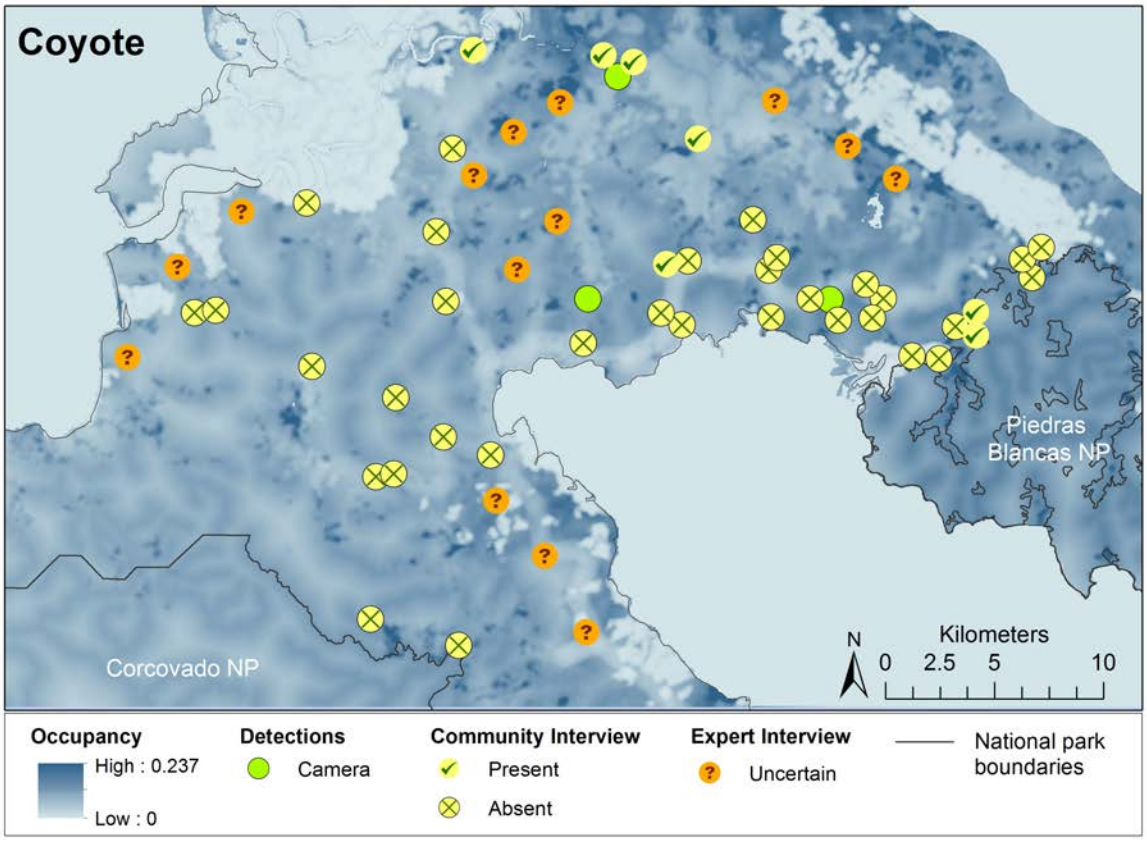


Figure 7.9 Map displaying coyote (*Canis latrans*) distribution using multiple sampling methods (camera trap, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays species occupancy based on occupancy modeling described in Chapter 5.

Primates

Camera Trap and Other Detection Data

The white-faced capuchin was the only primate detected at multiple camera trap sites (20 cameras totalling 37 detections). It was detected in all sampled habitats, except melina, reflecting the species' adaptability, though they were detected less frequently in forest than in other habitats (Table 5.3). In fact, the species was only detected by cameras in forests during one of the four sampling cycles (Table 7.3), though this detection occurred across seven sites. This finding may reflect a seasonal or periodic resource use of forest habitats by white-faced capuchins indicating that the species could be missed by camera traps in forests during rapid assessments.

The mantled howler monkey was detected by one forest site camera trap (after 2,700 trap days). However, Geoffroy's spider monkey and Central American squirrel monkey were not detected by the camera trap surveying.

Interview Data

The expert predicted white-faced capuchins and mantled howler monkeys to be present across the study area where suitable habitat was available. He was knowledgeable about habitat for all primate species: forest, secondary growth, *Raphia* and mangrove for white-faced capuchins; dense and secondary forest for mantled howler monkeys; dense forest for Geoffroy's spider monkey; and seasonally inundated forest, river edge and floodplain forest, and secondary forest for the Central American squirrel monkey. He successfully confirmed the presence of Geoffroy's spider monkey in the west of the study area, but was uncertain of its presence in west, which was confirmed by direct sightings of my camera trap survey team (Figure 7.12). The two locations where he was certain of the presence of the Central American squirrel monkey were corroborated by interview data, but he was uncertain of their presence throughout the majority of the study area.

Community interview data reflected an expected pattern of primate distribution based on known habitat for each species. For instance, white-faced capuchins (Figure 7.10) and howler monkeys (Figure 7.11) are prevalent and easy to detect and both species were almost unanimously reported present across the study. I expected Geoffroy's spider monkey (Figure 7.12) and the Central American squirrel monkey (Figure 7.13) to be less common and have more restricted distributions as they are currently listed as threatened by the IUCN. The community interview data corroborated this expectation by frequently reporting these species as absent in the study area.

Summary

As expected, cameras set for surveying terrestrial species are not very useful for surveying largely arboreal primates. Although when using camera traps I detected the white-faced capuchin in all main habitats sampled, community interviews were more expedient and reliable for confirming the presence of this species. As with the capuchin, community interviews were also more effective for determining the

presence of the other three primate species. This finding was expected given the ongoing presence of community members in forests occupied by these species, the conspicuous diurnal activity of primates, and the ease with which each of these species can be observed. Finally, the expert interview assisted with determining the presence of the two threatened primates at specific locations, but was limited for determining their distribution across the study area.

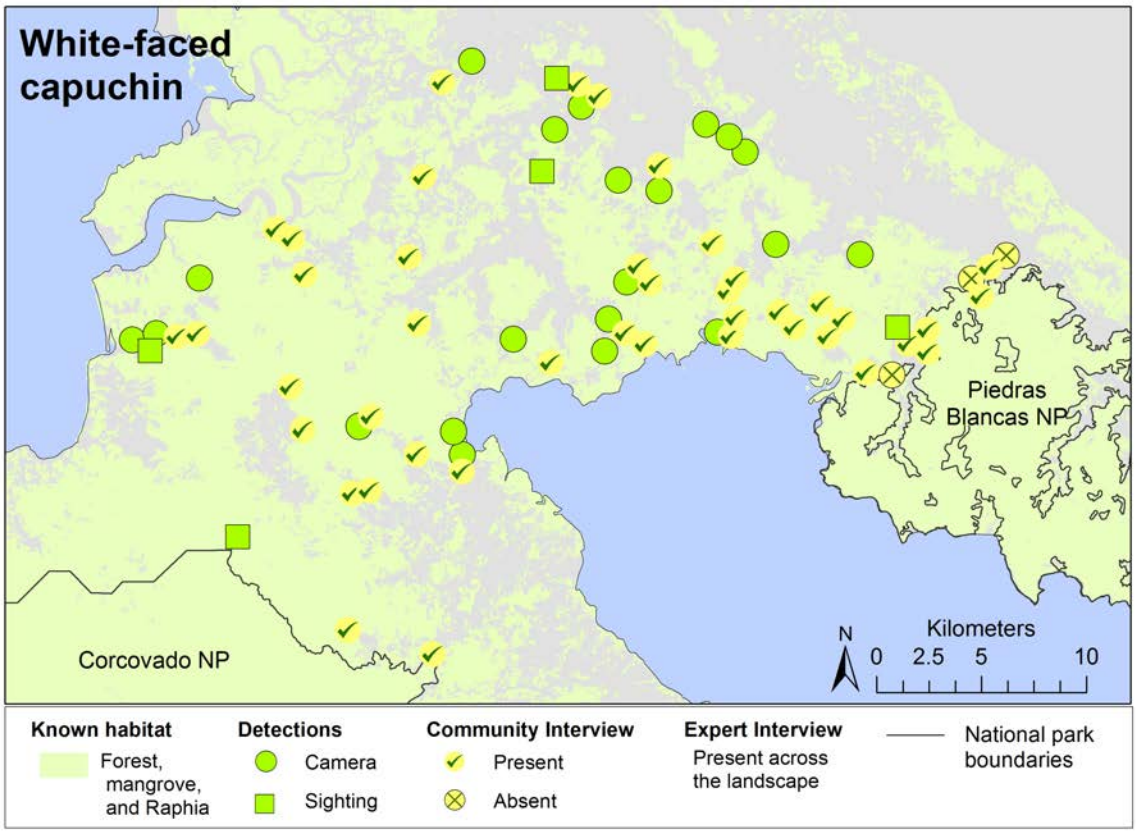


Figure 7.10 Map displaying white-faced capuchin (Cebus capucinus) distribution using multiple sampling methods (camera trap, direct sightings, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review and camera trap data from this study.

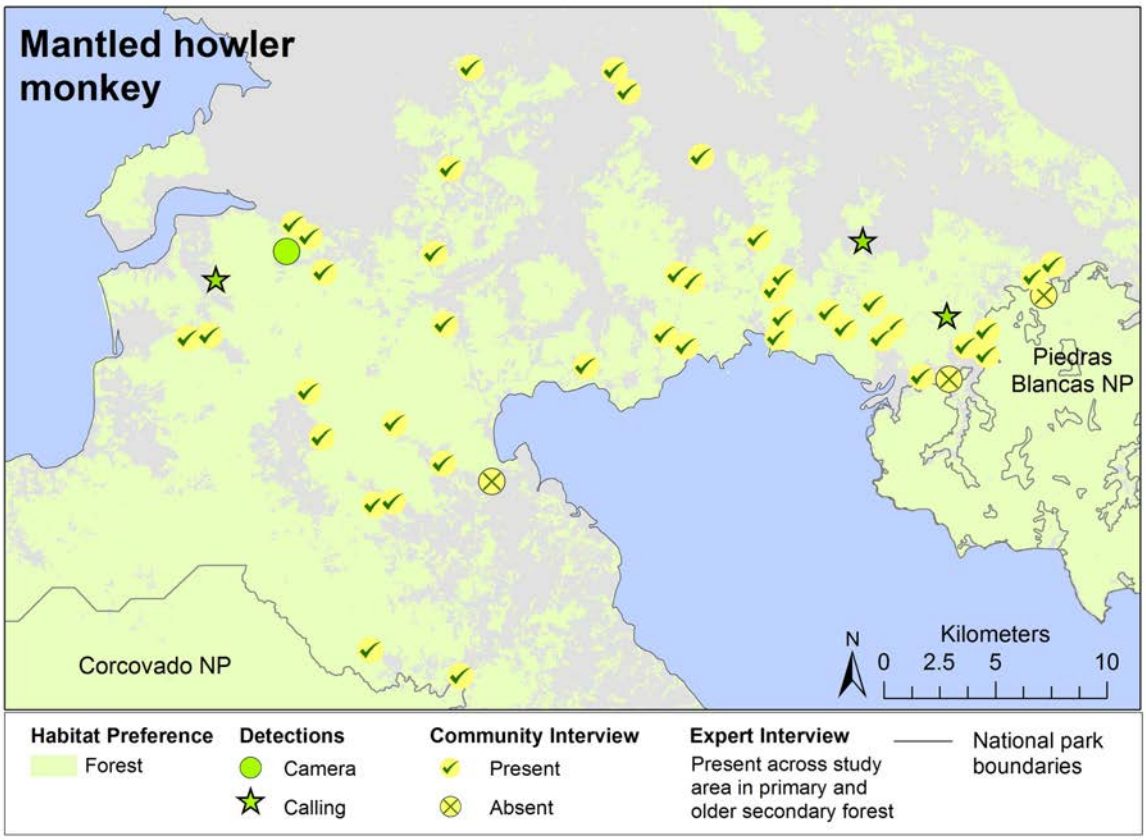


Figure 7.11 Map displaying mantled howler monkey (*Alouatta palliata*) distribution using multiple sampling methods (camera trap, call detections, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review.

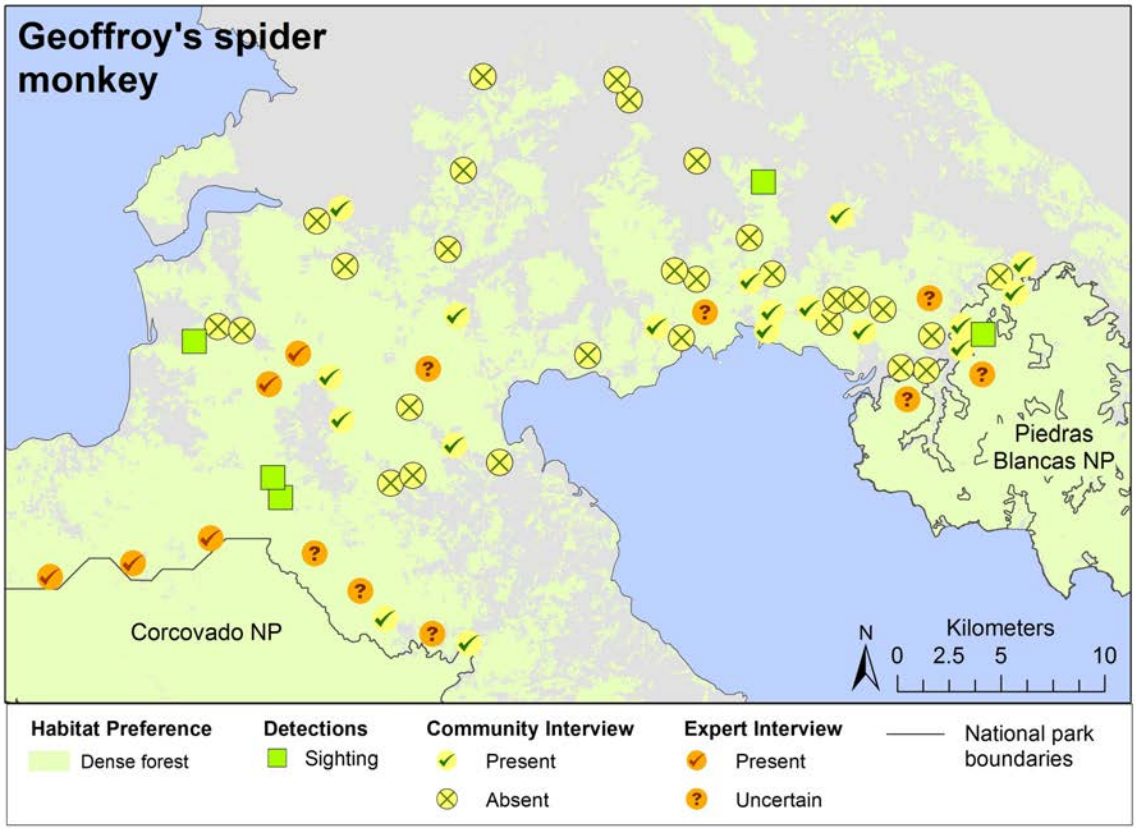


Figure 7.12 Map displaying Geoffroy's spider monkey (Ateles geoffroyi) distribution using multiple sampling methods (direct sightings, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review.

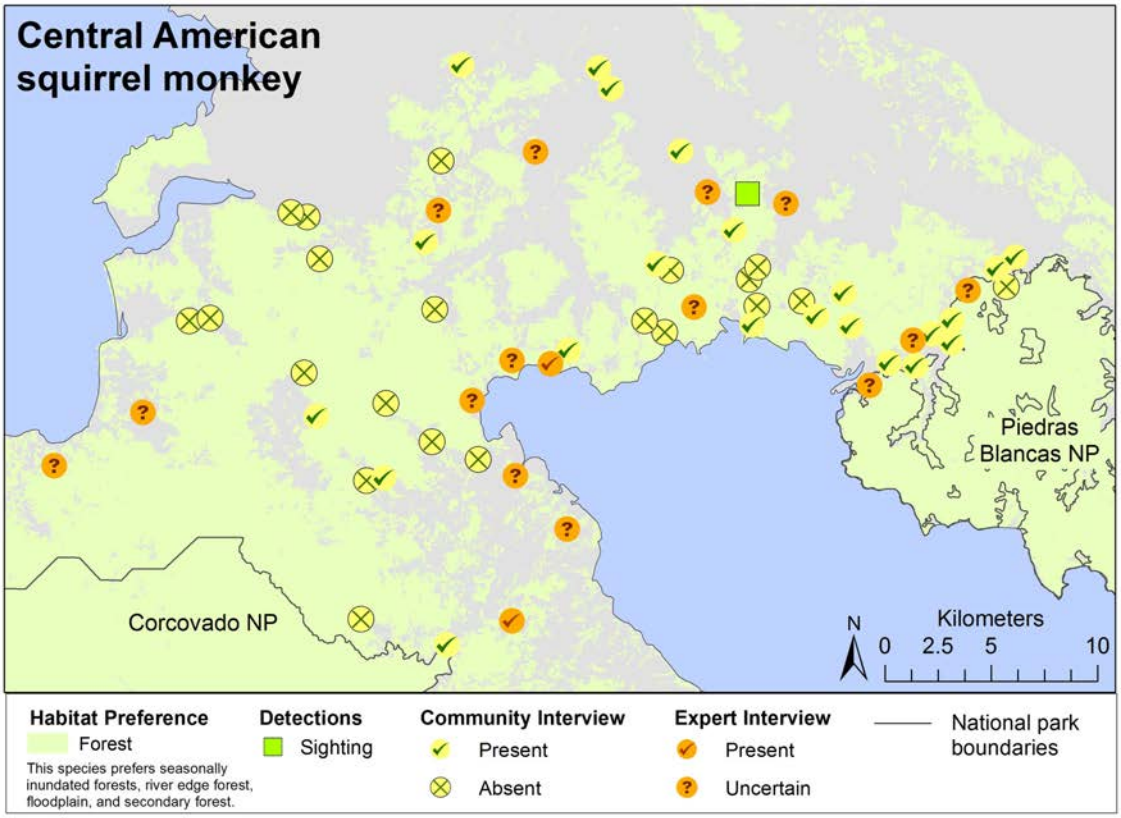


Figure 7.13 Map displaying Central American squirrel monkey (*Saimiri oerstedii*) distribution using multiple sampling methods (direct sightings, community interviews and expert interview) on the Osa Peninsula, Costa Rica. The base layer displays potential habitat for the species based on literature review.

Table 7.3. Summary of the reliability of each survey method for each species based on accuracy for interview results and survey effort for camera traps. Scoring criteria range from 1-3, three being the most reliable or preferred method (represented in dark green in the table). Scoring criteria are presented in the table footnote.

Species	Community interview	Expert interview	Camera	Notes on signs/ sightings/ calls
Collared peccary	3 – Correctly reported present across the study area.	2 – Correctly reported prevalent in east. Uncertain of presence in west; cameras confirmed its presence.	3 – Detected across the study area. Prevalent in east. Readily detected by cameras.	Difficult to distinguish between tracks of the two peccary species tracks. Infrequent direct encounters.
White-lipped peccary	2 – Much less prevalent than the collared peccary. Mostly reported absent. Both align with camera data.	3 – Present in CNP. Informed on seasonal and historical migrations, possibly explaining absence in cameras.	2 – Readily detected by cameras when present. Potential to miss if not sampling all seasons.	Difficult to distinguish between tracks of the two peccary species tracks. Infrequent direct encounters.
Puma	1 – Likely confused with jaguar tracks/signs. Mostly reported absent, contrary to camera data.	1 – Limited knowledge of distribution. Aware of community confusion with jaguar signs.	3 – Confirmed presence across the study area though took a relatively high survey effort.	Tracks easily detectable, but can be confused with jaguar. Rare to encounter directly.
Jaguar	2 – Aligned well in areas where detected by cameras. Confusion with puma likely based on the lack of puma reports.	3 – Reliable collective knowledge from researcher and resident reports. Cameras clarified uncertain areas.	2 – Confirmed in study area. Not detected in west, though species known to this area. High survey effort to detect.	Tracks easily detectable, but can be confused with puma. Rare to encounter directly.
Red brocket deer	2 – High correlation with camera data, except in north of study area.	2 – Uncertain of the species presence in the north of the study area – location where not detected by cameras.	3 – More prevalent in east and west ends of study area. Readily detected in forest.	Tracks distinct, but small and often obscured by leaf litter so can be difficult to detect.
White-tailed deer	3 – Accurately identified where confirmed by cameras. Other plausible locations identified.	NA	2 – Readily detected by cameras. Recorded in new habitat (*Raphia*). Possibly missed in some areas.	Tracks distinct and easy to detect.
Tapir	2 – Well aligned with camera data, except in two locations where erroneously largely reported absent.	3 – Well aligned with camera data. Two uncertain areas confirmed by cameras.	3 – Confirmed in study area, including locales missed by interviews. Not detected where tracks confirmed.	Tracks easy to identify and detect. Rarely encountered directly.
Coyote	2 – Reported	1 – No reports in	3 – Very informative	Potential to hear

Species	Community interview	Expert interview	Camera	Notes on signs/ sightings/ calls
	present in some locales where cameras detected, though mostly reported absent in these areas.	the area, though identified possible areas.	in confirming presence in areas where most respondents thought absent.	calls, but tracks can be mistaken with domestic or feral dogs.
White-faced capuchin	3 - Accurate that the species is present across the study area.	3 – Accurate that the species is present across the study area.	2 – Quickly detected at forest sites, but only in one sampling cycle. If forest use seasonal, might not detect rapidly.	Easily visible during daytime surveys and frequently encountered.
Geoffroy's spider monkey	3 – Distinct species, readily seen when present, makes residents best informed on species presence.	2 – Knew of species presence in the east, but was uncertain in the west. Reports on hunting of this species.	1 – Arboreal, not detected by camera	Detectable during day time surveys if present.
Central American squirrel monkey	3 – Easily detected when present, making residents likely the best informed on species presence.	2 – Predictions made on reports of locales and habitat use but was uncertain of presence.	1 – Largely arboreal, not detected by cameras	Detectable during day time surveys.
Mantled howler monkey	3 – Distinct calls easily heard making residents likely the best informed on species presence.	2- Predicted presence agrees with community interviews and known habitat.	1 – Largely arboreal. Only detected once by camera.	Easily detected by call.

Scoring for community and expert interviews are based on degree of alignment with camera trap survey data and usefulness of information not provided by cameras:

3 = Well aligned with camera data; information provides important additional information about species distribution; and/or provides the best information available of the three methods.

2 = Relatively well aligned with camera data, yet some clear misalignment or knowledge gaps; Information provided insightful, but not essential, addition information to camera data.

1 = Not well aligned with camera data, or extensive disagreement about the species presence in community interviews.

Scoring for camera trap survey data is based on the time until first detection (TFD) (i.e., number of trap days to detect a species) and importance in relation to interview data. Trap days are a collective total for the sampling cycle; for example, 10 cameras set for 5 nights equals 50 trap days.

3 = Quickly detected (average TFD <250 trap days of sampling in known habitat); was the most reliable method of identification; and/or provided important location information missed by interviews.

2 = Medium detection rate (TFD >250 trap days).

1 = Very slow detection rate (TFD >500 trap days), or not detected, but species likely present.

Table 7.4. Summary of camera trap effort (time to first detection, or TFD) for each targeted mammal species in the study area located on the Osa Peninsula, Costa Rica. Detection summarizes camera trap effort in preferred habitat - forest for all species, with two exceptions noted in the table. The focus on forest cameras is with the intention of reflecting camera placement in an HCV rapid assessment scenario, which is most likely to focus on sampling remaining forest in or surrounding a proposed development.

Species	Number of trap days (time) to first detection (TFD) in overall study	Average number of trap days (time) to first detection (TFD) during the survey cycle where detected	No. of cycles in which the species was detected (max. of 4)	Sirena Research Station - Number of trap days (time) to first detection (TFD)
White-lipped peccary	Not detected	Not Applicable	1	30
Red brocket	42	174	4	18
Collared peccary	53	230	4	12
White-faced capuchin	89	89	1	Not detected
Puma	488	389	4	Not detected
Coyote^	555	54	1	Not detected
White-tailed deer*	593	188	2	Not detected
Tapir	920	78	3	12
Jaguar	1056	185	3	Not detected
Mantled howler monkey	2737	772	1	Not detected

^ While coyote habitat preferences vary widely depending on region, only grassland and oil palm cameras were included in the analyses to reflect the habitat types where the species was detected during this study.

* Cameras placed in grassland and *Raphia* habitat types were included in these calculations to reflect this species' preference for relatively open, sparsely vegetated habitats (and habitats where the species was detected in this study).

Conclusion

The survey method comparison in this chapter highlights that all three survey methods – camera trapping, community interviews and expert interviews – are often informative and complimentary, but when viewed together provide a more comprehensive understanding of species distribution than any survey technique performed in isolation. Occasionally an individual survey technique is likely to provide better results and could lead to reduced survey effort when compared with others. However, no one method stood out as performing well above the others for all species in all locations. This highlights the need for a multifaceted approach for undertaking rapid mammal surveys. The study confirms the usefulness of interview data for HCV

rapid mammal assessments aimed at establishing a species inventory and gaining insight into species distributions.

Camera trap surveying was highly effective for identifying the presence of half of the species considered. Survey time (trap days to first detection) and thus required survey effort was the greatest limitation for this method. Additionally, camera traps not specifically targeted at primates were unlikely to detect these species. Target species and locations for camera trap surveys should be selected carefully to confirm the presence of species unlikely to be confirmed satisfactorily via community and expert interviews, for example, pumas in this study. The cost to purchase and time to set cameras can also limit the effectiveness of camera trap surveying.

Community interviews were also ranked as highly effective for half of the mammal species considered, proving to be most informative for primates, but least reliable for species whose tracks are easily confused (e.g., puma with jaguar and collared peccary with white-lipped peccary). Camera trapping would be an ancillary survey approach that could confirm the presence of these species and in some cases (e.g., peccaries) detect them relatively quickly.

Expert interviews can not only provide local context but also, in this study, the expert interview was the most informative rapid technique for inferring distribution of flagship species that are priorities for conservation in the area – i.e., jaguar, tapir and white-lipped peccary. Expert knowledge on seasonal use patterns and specific management issues (e.g., hunting and human-wildlife conflict) can as be particularly useful as additional underlying information influencing current species distribution patterns. When exposed to survey time limitations, knowledgeable land managers and researchers with extensive experience in a given area can provide valuable species distribution information. Unfortunately, the capacity of protected area management staff in tropical regions is often resource limited (Bruner et al. 2004).

Knowledge and capacity of community and expert interview respondents must be carefully considered when using interview data (Hellier et al. 1999, Can and Togan 2009, this study). Costa Rica is unusual amongst tropical countries, well known for its expansive protected area system and environmentally friendly policies (Andam et al.

2010, Pagiola 2008). On the Osa Peninsula, the protected area management authority (SINAC-ACOSA) is active and engaged with stakeholders (including residents and researchers) on wildlife management. Many residents are involved in the ecotourism industry and hunt for food and sport (peccaries, paca and spider monkey the preferred species) (Carrillo et al. 2000, Jimenez 2012). This has created an unusually knowledgeable populace with regard to wildlife, which is important to consider when extrapolating the documented competence of interview respondents on the Osa Peninsula to that of other regions.

HCV rapid mammal assessment recommendations

As stated in the Introduction of Chapter 1, the research for this thesis was intended to benefit HCV practitioners and scientists—evaluating evidence of mammal use of biological corridors and non-forest habitats in fragmented landscapes and providing insight into the efficacy of widely used rapid-sampling methods. Based on (1) the results from this chapter and Chapter 3, (2) lessons learned from conducting the research presented in this thesis, and (3) personal experience conducting rapid mammal surveys for HCV assessments and reviewing other such assessments, I conclude this chapter with the following list of considerations when designing and implementing HCV rapid mammal surveys using the sampling methods discussed in this chapter.

Determining target species and sampling method

1. A list of all mammal species in the broad geographic region of the proposed development should be created prior to field survey. The list should identify High

Conservation Value mammal species[1] potentially present in the proposed development area based on known regional distribution and land cover data (i.e. potential habitat) in the proposed development area and surrounding landscape.

2. From this list, target survey species should be selected prior to survey based on the likelihood of a species to influence how assessors make conservation design recommendations for a proposed development area. For example, larger mammals that have larger home range requirements, such as elephants, or species that rely heavily on contiguous forest, such as arboreal primates, are likely to have a stronger influence on conservation design outcomes than species with smaller home ranges or that are habitat generalists. Important prey for an HCV species might also be a target survey species.
3. Survey design and method selection for each species should be selected based on the method(s) that is most likely to provide reliable data for the selected target species. Initial method selection can be determined based on the surveyor's prior knowledge of the mammal community in the survey area and literature review, identifying species that will possibly be confused during community interviews, survey effort likely necessary to detect with camera traps (if these are an option), etc.

Expert interviews

4. Experts come in many forms – including local land managers, hunters, researchers, and guides. Where possible it is best to interview experts prior to field survey to

[1] HCV species are species that meet one or more of the following criteria: (1) **Rare**: Naturally rare, existing only at very low densities in undisturbed habitat; Rare because of human activities e.g. habitat destruction, overhunting, climate change; Or at the limit of their natural distribution (even if they are common elsewhere); (2) **Threatened**: Species classified by IUCN as Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) at a global or regional level, or whose trade is regulated under international agreements (e.g. CITES), as well as nationally protected species; (3) **Endemic**: Found within a restricted geographical region, which may range from a unique site or a geographical feature (such as an island, a mountain range or river basin), to a political boundary such as a province or country (HCVRN 2013).

help identify priority survey areas and species-specific conservation issues, guide camera trap placement (if used) and solicit input on community interview design.

5. Locally based experts (e.g., hunters) should be sought out for interview on site where not available in advance of the field survey.
6. For experts that are map literate, it is most informative to discuss mammal species distributions in the assessment area and broader landscape (i.e., the area extending at least 2 km outside of the assessment area and beyond to include any large blocks of natural areas and the nearest protected areas) while viewing a land cover map of the area with the expert.

Community interviews

7. Community interviews are informative but if unstructured can be very time consuming depending on the local culture and the number of species being discussed. Each conversation can entail extensive cordialities and appropriate cultural practices. It is recommended that a short, focal list of species are decided upon prior to survey (as discussed above) and survey questions limited to these species.
8. During interviews it is important to communicate clearly about the spatial structure of a landscape (e.g., blocks of forest), and to be explicit about presence in the broader landscape versus presence at certain locales. The local names of forest blocks and reference locations should be established *a priori* to aid in linking responses to locations.
9. Locally used names for all species should be identified prior to survey where possible (in discussion with a regional expert). If this is not possible, then such clarification should be sought during initial interviews to facilitate communication and understanding in subsequent interviews.
10. Opportunistic questioning of people in passing (informal interviews, without the use of a sit-down interview with a data sheet) should also be employed for priority species to acquire as much data as possible and use time and resources efficiently. A streamlined set of species and questions should be established for such opportunistic data collection.

11. Other taxonomic specialists involved in the HCV survey (e.g., botanists) and the social survey team should be informed of the priority species for the mammal survey, and asked to record information obtained regarding these species while they are undertaking their surveys.
12. If species that are easily confused with similar species are included on the interview list, the interview process should be carefully designed and carried out, with side-by-side images of the similar species for reference in conversation, to provide clarity. Results should also be interpreted with a high degree of caution. Examples of such species include peccary, medium-sized feline species, and, in Asia, leaf monkeys (*Trachypithecus* spp.).
13. Mobile phone cameras are becoming increasingly common in rural areas. It is useful to ask people, including plantation employees, if they have photos of any local wildlife as well as remnants of species that have been hunted or are being kept for food, pets or trade.
14. Community (and expert) interviews allow for information gathering on seasonal resource use by target species. Where such behavioral seasonality is thought to occur, associated questions should be posed to interview respondents to identify the location and potential importance of the seasonal resource.

Camera trapping

15. Cameras traps should be used to target terrestrial species that are of conservation concern or immediately related to them (e.g., primary prey species); particularly those likely to be difficult to verify through interview surveys. Camera trap surveying can also be used to validate questionable interview data. Cameras should be set in locations most likely to detect the target species and left in place for as long as possible to increase the likelihood of detection.
16. In addition to targeting specific species, cameras can be useful for comparing species abundance and diversity between habitats or particular locations (Benchimol 2016). Where time allows, this is an effective use of cameras traps.
17. It is possible that cameras will need to be deployed for a period of time beyond the rapid assessment to confirm presence of a target species. In such cases, while there is still uncertainty about a target species' presence, precautionary

management measures (no conversion of potential habitat) should be recommended until questions regarding a species presence and distribution are satisfactorily answered by cameras or other methods deemed sufficient.

Direct observations

18. Direct (sightings) and indirect (tracks, scat, signs, calls, etc.) observations readily complement the other data collection methods described in this chapter and should be recorded while employing the other methods (e.g., while traversing the study area to get to villages, conducting reconnaissance walks in forest blocks to assess habitat quality or setting camera traps).
19. Survey methods focusing on direct and indirect observations (e.g., line transects or targeted searches of known habitat or location for a species) can also be implemented where deemed the most informative method, especially in targeted locations or habitats. Using a local hunter or knowledgeable resident as a guide can increase the rate of track and sign detection, assist in identification and facilitate informative conversations about the distribution and resource use of target species.
20. Systematic line transects across a proposed development area are sometimes used in rapid HCV mammal assessments and can be very informative, but are also time and labor intensive. Although more scientifically rigorous, when used in isolation for rapid HCV mammal assessments, line transect data for mammals are often limited to certain species and record few, if any, detections of target species (as defined above). These data often result in a comparison of the presence and abundance of common species in different types of habitats (e.g., to compare mixed forest and agricultural landscapes). This approach is ineffective for HCV surveys where the aim is to present an informed logic and conclusion on the distribution of identified priority species and back this conclusion with multiple data sources. Line transects should therefore be used as part of a multi-faceted assessment approach to complement the survey methods discussed in this chapter, prioritizing and utilizing the method only where it will be an effective use of time and resources and contribute to a comprehensive understanding of mammal presence and the distribution of target species in the landscape.

Chapter 8 Synthesis

Maintaining connectivity for tropical rainforest mammals in fragmented, mixed-agricultural landscapes is a challenging, multi-faceted issue. The variability between large mammal species' habitat needs and other environmental and anthropogenic variables that are likely to influence how large mammals move through a landscape are only the beginning of the challenges biologists and environmental managers face when designing biological corridors (Chapter 2). The array of methods and analysis decisions to be made when modelling connectivity (spatial scale, defining resistance, and integration of multiple species results) further complicated the design of biological corridors. Even once these hurdles are overcome, there may be minimal uptake of modeled data unless the important exercise of effectively bringing together the relevant regional stakeholders including scientists, public stakeholders, and policy makers has taken place (McShea 2014, Beier et al. 2007).

Time limitations can prevent adequate investigation of large mammal communities and landscape connectivity for large mammal species (Chapters 1 and 7). In rapid assessment scenarios, such as *Acacia* and oil palm plantation development, time and skill limitations prevent assessors from undertaking much of the scientifically backed survey design and analysis methods for modelling connectivity (Chapters 2 and 5). Although it has been said that there are no universal rules to corridors (Chetkiewicz et al. 2006) and the creation of uniform guidelines is neither possible nor desirable (Bennett 2003), the rapid pace of land conversion and plantation development in many tropical countries requires the development of some "rules of thumb" for corridor design when time and comprehensive empirical data are not available to guide decision making. With these challenges in mind, this thesis met its original objectives by (1) identifying corridor design variables likely to influence the use of biological corridors by large mammals in tropical landscapes, (2) testing selected corridor design variables in two disparate tropical landscapes, and (3) exploring the efficacy of three rapid assessment techniques for use in rapid assessment scenarios.

My literature review indicates that landscape scale corridors are a popular conservation strategy in tropical countries, but much of scientific literature on the effectiveness of tropical forest corridors is undertaken at a much smaller spatial scale. The scale of these studies precludes an effective analysis of broader ecological processes across extensive forest landscapes. Studies of large mammals in tropical countries largely support the recommendations for corridor design from the more extensive body of literature on temperate area corridors. In particular they suggest corridor usage by large mammals may be positively impacted by: allowing for species-specific responses to corridors; ensuring direct connectivity via corridors which is known to increase species richness and abundance in forest fragments; and maintaining habitat quality in the corridor which is important for corridor functionality. Further anthropogenic disturbances (hunting, logging, transport corridors, settlements, and mining) of corridors and spatially proximate forests are well known have a clear negative impact on corridor use. However, throughout the examined literature corridor width and length were infrequently studied. It is expected that tropical corridors aiming to maintain species richness in the landscape will need to be wider than those in temperate region due to a higher number of forest interior specialists in tropical regions and the higher level of vulnerability of tropical forests to edge effects (de Lima and Gascon 1999). The few studies that were conducted on corridor length identified species specific effects.

In Chapter 4, I examined linear remnants of riparian forest within an *Acacia* plantation to evaluate five corridor-design variables for large (>1 kg) mammals in Sumatra. The variables I evaluated were corridor width, corridor length, corridor distance from core habitat, direct connectivity with core habitat, and habitat type. I found that linear riparian remnants are utilized as habitat and localized movement corridors, extending up to a few kilometers in length, for many large mammal species in Sumatra. These examined corridors of remnant native riparian forest ranged from 100-200 m in width, which appears to be a reasonable minimum width for riparian buffers to serve as movement corridors for large Sumatran mammals. However, it goes without saying that corridors of this width would experience reduced habitat quality though edge effects. The reduction in habitat quality would be especially apparent during harvest

rotations when the buffering effects of the plantation is temporarily denuded exposing remnant corridors to wind, microclimatic stresses, and additional environmental and anthropogenic pressures. If reducing the influence of edge effects on riparian corridors were a conservation priority, much wider corridors would be required preferentially in conjunction with the maintenance of adjacent land covers (such as mature *Acacia*). Small breaks in habitat connectivity (e.g., service roads) did not appear to impede the movement of most large, terrestrial mammals, though wider breaks in connectivity significantly restricted the dispersal of some species. This study was the first to assess the habitat and landscape factors that influence the use of linear remnants by the Malay tapir. I found that that tapir use of linear remnants increases with remnant width and the availability of native forest habitat within the remnant. I also found that tapirs venture deep into *Acacia* plantations, travelling up to 3.75 km along high-contrast linear remnants, using remnants with greater intensity as they travel farther from core habitat. These findings will significantly contribute to the management of Malay tapirs in mixed forest and agricultural landscapes.

On a much larger scale, in Chapters 5 and 6 I examined a 740 km^2 area of the Osa Biological Corridor in Costa Rica. Within this area, I evaluated the influence of two corridor-design variables, species habitat use and distance to core habitat areas, on 16 large mammal species. This study identified species-specific abundance responses to each of the seven habitats types analyzed. In particular, however, forest presence had a strong effect on habitat occupancy for almost all species. Conversely, distance to large blocks of forest (≥500 ha) only significantly impacted the occupancy rates of five species. Many of the examined species responded negatively to the percent of mangroves, grasslands and oil palm surrounding sample sites though felids did were not significantly deterred by oil palm. Modeled species distributions showed that primary forest presence was a clear positive driver of occupancy for most species though a wide range of occupancy probability was found between species and study area locality. The presence of strong correlations between mapped connectivity measures for each individual species (using circuit flow analysis) with the averaged value for all species, suggests little need for trade-offs among different species when selecting priority areas for maintaining landscape connectivity for forest-dependent

mammals. The integrated approach of intensive landscape scale sampling with camera traps, multi-species occupancy modeling and corridor modelling in this study is a cost-efficient approach and especially useful for defining regional corridors between protected areas at a scale of a few 100 to 1000 km^2.

In Chapters 2 and 7 I compared three rapid assessment techniques - baiting camera traps, community interviews and expert interviews - to identify their efficacy for High Conservation Value rapid mammal assessments. In particular, I compared their value in creating an accurate regional species inventory and the identification of species distribution across a landscape. All three methods showed varying efficacy which was often species-specific though each technique was deemed useful for HCV rapid mammal assessments. For instance, in Sumatra using a paired study design I identified that camera traps baited with sent lures perform better than unbaited traps when detecting rainforest mammals. Further, based on my comparison of camera trapping data with community and expert interviews in Costa Rica, these interviews can be effective rapid survey techniques for some large mammal species potentially leading to a reduction in the required survey effort. However, while each survey technique contains merit a comprehensive understanding of mammal species presence and distribution within a landscape requires a diversified approach, not reliant on a single survey technique.

Collectively, my thesis findings significantly further our understanding of biological corridor-design variables for large tropical mammals and the effectiveness of rapid assessment techniques for mammal species presence and distribution within tropical landscapes. The results and associated management recommendations I provide in each chapter are readily applicable for assessment and management scenarios which aim to maintain landscape connectivity for large mammals in heterogeneous tropical landscapes.

References

ABARES. 2012. Type and extent of Australia's forests. Forests Australia http://adl.brs.gov.au/forestsaustralia/facts/type.html.

Abood, S. A., J. S. H. Lee, Z. Burivalova, J. Garcia‐Ulloa, and L. P. Koh. 2015. Relative contributions of the logging, fiber, oil palm, and mining industries to forest loss in Indonesia. Conservation Letters 8(1): 58-67.

Abrahms, B., S. C. Sawyer, N. R. Jordan, J. W. McNutt, A. M. Wilson, and J. S. Brashares. 2017. Does wildlife resource selection accurately inform corridor conservation? Journal of Applied Ecology 54(2): 412-422.

Adriaensen, F., J. P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64(4): 233-247.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19(6): 716-723.

Almeida, S. M., L. C. Silva, M. R. Cardoso, P. V. Cerqueira, L. Juen, and M. P. D. Santos. 2016. The effects of oil palm plantations on the functional diversity of Amazonian birds. Journal of Tropical Ecology 32(6): 510-525.

Altrichter, M., and R. Almeida. 2002. Exploitation of white-lipped peccaries *Tayassu pecari* (Artiodactyla: Tayassuidae) on the Osa Peninsula, Costa Rica. Oryx 36(2): 126.

Andam, K. S., P. J. Ferraro, K. R. E. Sims, A. Healy, and M. B. Holland. 2010. Protected areas reduced poverty in Costa Rica and Thailand. Proceedings of the National Academy of Sciences 107(22): 9996-10001.

Barlow, J., T. A. Gardner, I. S. Araujo, et al. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America 104(47): 18555-18560.

Barlow, J., J. Louzada, L. Parry, M. I. M. Hernandez, J. Hawes, C. A. Peres, F. Z. Vaz-de-Mello, and T. A. Gardner. 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. Journal of Applied Ecology 47(4): 779-788.

Bartley, T. 2003. Certifying forests and factories: States, social movements, and the rise of private regulation in the apparel and forest products fields. Politics & Society 31(3): 433-464.

Bartley, T. 2007. How foundations shape social movements: The construction of an organizational field and the rise of forest certification. Social Problems 54(3): 229-255.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using S4 classes.

Beck–King, H., O. v. Helversen, and R. Beck–King. 1999. Home range, population density, and food resources of Agouti paca (Rodentia: Agoutidae) in Costa Rica: a study using alternative Methods1. Biotropica 31(4): 675-685.

Beier, P., and S. Loe. 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildlife Society Bulletin 20(4): 434-440.

Beier, P., D. Majka, and J. Jenness. 2007. Conceptual steps for designing wildlife corridors. Northern Arizona University, Flagstaff, Arizona, USA.

Beier, P., D. R. Majka, and S. L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications 19(8): 2067-2077.

Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: Choices in procedures for designing wildland linkages. Conservation Biology 22(4): 836-851.

Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12(6): 1241-1252.

Benchimol, M. 2016. Medium and Large-sized Mammals.*in* T. H. Larsen, editor. Core Standardized Methods for Rapid Biological Field Assessment. Conservation International, Arlington, VA.

Bennett, A. 2003. Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. International Union for Conservation of Nature, Gland, Switzerland and Cambridge, United Kingdom.

Borthakur, U., R. D. Barman, C. Das, A. Basumatary, A. Talukdar, M. F. Ahmed, B. K. Talukdar, and R. Bharali. 2011. Noninvasive genetic monitoring of tiger (Panthera tigris tigris) population of Orang National Park in the Brahmaputra floodplain, Assam, India. European Journal of Wildlife Research 3(57): 603-613.

Breckheimer, I., N. M. Haddad, W. F. Morris, A. M. Trainor, W. R. Fields, R. Jobe, B. R. Hudgens, A. Moody, and J. R. Walters. 2014. Defining and evaluating the umbrella species concept for conserving and restoring landscape connectivity. Conservation Biology 28(6): 1584-1593.

Broadbent, E. N., A. M. Almeyda Zambrano, R. D. Dirzo, S. L. Almeyda Zambrano, C. A. Quispe Gil, L. Morales Barquero, M. Villalobos, C. Hunt, and C. Menke. 2013. INOGO Mapas 2013: A high resolution map of land cover in the Osa Peninsula and Golfito region of Costa Rica. The Woods Hole Institute for the Environment, Stanford University, CA.

Brodie, J. F., A. J. Giordano, B. Dickson, M. Hebblewhite, H. Bernard, J. Mohd‐Azlan, J. Anderson, and L. Ambu. 2015. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conservation Biology 29(1): 122-132.

Brown, E., N. Dudley, A. Lindhe, D. Muhtaman, C. Stewart, and T. Synnott. 2013. Common guidance for the identification of High Conservation Values. HCV Resource Network.

Brown, M. 2011. Paper/Tiger. Foreign Correspondent. Australian Broadcast Corporation.

Bruner, A. G., R. E. Gullison, and A. Balmford. 2004. Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. BioScience 54(12): 1119-1126.

Bueno, A. S., R. S. Bruno, T. P. Pimentel, T. M. Sanaiotti, and W. E. Magnusson. 2012. The width of riparian habitats for understory birds in an Amazonian forest. Ecological Applications 22(2): 722-734.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2 edition. Springer-Verlag, New York.

Burton, A. C., M. K. Sam, C. Balangtaa, and J. S. Brashares. 2012. Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. PLoS ONE 7(5): e38007.

Butler, R. A., and W. F. Laurance. 2008. New strategies for conserving tropical forests. Trends in Ecology & Evolution 23(9): 469-472.

Can, Ö. E., and İ. Togan. 2009. Camera trapping of large mammals in Yenice Forest, Turkey: local information versus camera traps. Oryx 43(3): 427-430.

Carbone, C., S. Christie, K. Conforti, et al. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation 4(1): 75-79.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science 309(5738): 1239-1241.

Carlson, K. M., L. M. Curran, D. Ratnasari, et al. 2012. Committed carbon emissions, deforestation, and community land conversion from oil palm plantation expansion in West Kalimantan, Indonesia. Proceedings of the National Academy of Sciences 109(19): 7559-7564.

Carney, J., and M. Hiraoka. 1997. Raphia taedigera in the Amazon Estuary. Principes 41(3): 125-130.

Carrillo, E., T. K. Fuller, and J. C. Saenz. 2009. Jaguar (Panthera onca) hunting activity: effects of prey distribution and availability. Journal of Tropical Ecology 25(05): 563-567.

Carrillo, E., J. C. Saenz, and T. K. Fuller. 2002. Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. Biological Conservation 108(3): 317-324.
Carrillo, E., G. Wong, and A. D. Cuaron. 2000. Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. Conservation Biology 14(6): 1580-1591.
Chetkiewicz, C.-L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46(5): 1036-1047.
Chetkiewicz, C. L. B., C. C. S. Clair, and M. S. Boyce. 2006. Corridors for conservation: Integrating pattern and process. Pages 317-342 Annual Review of Ecology Evolution and Systematics.
Collinge, S. K. 1996. Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landscape and Urban Planning 36(1): 59-77.
Colwell, R. K. 2006. EstimateS: statistical estimation of species richness and shared species from samples. University of Connecticut, Storrs.
Costa, C., V. H. F. Oliveira, R. Maciel, W. Beiroz, V. Korasaki, and J. Louzada. 2017. Variegated tropical landscapes conserve diverse dung beetle communities. Peerj 5: 22.
Cushman, S. A., M. Chase, and C. Griffin. 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. Pages 349-367 Spatial complexity, informatics, and wildlife conservation. Springer.
Cushman, S. A., and F. Huettmann. 2010. Spatial complexity, informatics, and wildlife conservation. Springer.
Cushman, S. A., and E. L. Landguth. 2012. Multi-taxa population connectivity in the Northern Rocky Mountains. Ecological Modelling 231: 101-112.
Cushman, S. A., J. S. Lewis, and E. L. Landguth. 2014. Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. Diversity 6(4): 844-854.
de la Pena-Cuellar, E., J. Benitez-Malvido, L. D. Avila-Cabadilla, M. Martinez-Ramos, and A. Estrada. 2015. Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape. Ecology and Evolution 5(4): 903-913.
de Lima, M. G., and C. Gascon. 1999. The conservation value of linear forest remnants in central Amazonia. Biological Conservation 91(2-3): 241-247.
Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14(2): 342-355.
DeClerck, F. A. J., R. Chazdon, K. D. Holl, J. C. Milder, B. Finegan, A. Martinez-Salinas, P. Imbach, L. Canet, and Z. Ramos. 2010. Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. Biological Conservation 143(10): 2301-2313.
DeMatteo, K. E., M. A. Rinas, J. P. Zurano, N. Selleski, R. G. Schneider, and C. F. Argüelles. 2017. Using niche-modelling and species-specific cost analyses to determine a multispecies corridor in a fragmented landscape. PLoS ONE 12(8): e0183648.
Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7(2): 129-146.
Díaz, A., E. Galante, and M. E. Favila. 2010. The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. Journal of Insect Science 10(81): 1-16.
Diaz-Gallegos, J. R., J. F. Mas, and A. V. Montes. 2008. Monitoring deforestation patterns in the Mesoamerican Biological Corridor, Mexico. Interciencia 33(12): 882-890.
Dickson, B. G., G. W. Roemer, B. H. McRae, and J. M. Rundall. 2013. Models of Regional Habitat Quality and Connectivity for Pumas (Puma concolor) in the Southwestern United States. PLoS ONE 8(12): e81898.

Dixo, M., J. P. Metzger, J. S. Morgante, and K. R. Zamudio. 2009. Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biological Conservation 142(8): 1560-1569.
Eadie, E. 2012. Feeding ecology and life history strategies of white-faced capuchin monkeys. University of New Mexico, Albuquerque, New Mexico, USA.
Emmons, L. H., and F. Feer. 1997. Neotropical Rainforest Mammals: A Field Guide. Second edition. The University of Chicago Press, Chicago, USA.
Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4): 714-724.
Estrada, A., P. Cammarano, and R. Coates-Estrada. 2000. Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. Biodiversity and Conservation 9(10): 1399-1416.
Estrada, A., and R. Coates-Estrada. 2001a. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. Ecography 24(1): 94-102.
Estrada, A., and R. Coates-Estrada. 2001b. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. Journal of Tropical Ecology 17(5): 627-646.
Ewers, R. M., R. K. Didham, L. Fahrig, et al. 2011. A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. Philosophical Transactions of the Royal Society B-Biological Sciences 366(1582): 3292-3302.
FAO. 2014. FAOSTAT Statistics Database. Retreived from
Field, A., J. Miles, and Z. Field. 2012. Discovering Statistics Using R. Discovering Statistics Using R. SAGE, London, United Kingdom.
Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16(3): 265-280.
Fischer, J., D. B. Lindenmayer, and A. D. Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4(2): 80-86.
Fischer, R. A., and C. J. Fischenich. 2000. Design recommendations for riparian corridors and vegetated buffer strips. Environmental Laboratory, US Army Engineer Research and Development Center, Vicksburg, MS.
Fitzherbert, E. B., M. J. Struebig, A. Morel, F. Danielsen, C. A. Bruhl, P. F. Donald, and B. Phalan. 2008. How will oil palm expansion affect biodiversity? Trends in Ecology & Evolution 23(10): 538-545.
Fleishman, E., J. Anderson, and B. G. Dickson. 2017. Single-Species and Multiple-Species Connectivity Models for Large Mammals on the Navajo Nation. Western North American Naturalist 77(2): 237-251.
Forman, R. T. T., and M. Godron. 1986. Landscape Ecology. John Wiley and Sons, New York.
FSC. 2014. FSC: increasingly relevant for tropical forests. Sustainable forest management: responding to local and global interests. The Forest Stewardship Council A.C., Bonn, Germany,.
FSC. 2015. FSC Principles and Criteria for Forest Stewardship. Forest Stewardship Council, Bonn, Germany.
Galanes, I. T., and J. R. Thomlinson. 2011. Soil millipede diversity in tropical forest patches and its relation to landscape structure in northeastern Puerto Rico. Biodiversity and Conservation 20(13): 2967-2980.
Gaveau, D. L. A., D. Sheil, Husnayaen, M. A. Salim, S. Arjasakusuma, M. Ancrenaz, P. Pacheco, and E. Meijaard. 2016. Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo.

Gerber, B. D., S. M. Karpanty, and J. Randrianantenaina. 2012. The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. Oryx 46(03): 414-422.
Gilbert-Norton, L., R. Wilson, J. R. Stevens, and K. H. Beard. 2010. A Meta-Analytic Review of Corridor Effectiveness. Conservation Biology 24(3): 660-668.
Gillies, C. S., H. L. Beyer, and C. C. St Clair. 2011. Fine-scale movement decisions of tropical forest birds in a fragmented landscape. Ecological Applications 21(3): 944-954.
Gillies, C. S., and C. C. St Clair. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. Journal of Applied Ecology 47(1): 182-190.
Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4(4): 379-391.
Gould, R. K., L. Pejchar, S. G. Bothwell, B. Brosi, S. Wolny, C. D. Mendenhall, and G. Daily. 2013. Forest Restoration and Parasitoid Wasp Communities in Montane Hawai'i. PLoS ONE 8(3): e59356.
Gray, C. L., B. I. Simmons, T. M. Fayle, D. J. Mann, and E. M. Slade. 2016. Are riparian forest reserves sources of invertebrate biodiversity spillover and associated ecosystem functions in oil palm landscapes? Biological Conservation 194: 176-183.
Gray, C. L., E. M. Slade, D. J. Mann, and O. T. Lewis. 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm-dominated tropical landscapes? Ecology and Evolution 4(7): 1049-1060.
Gregory, A. J., and P. Beier. 2014. Response variables for evaluation of the effectiveness of conservation corridors. Conservation Biology 28(3): 689-695.
Guillera-Arroita, G. 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. Ecography 40(2): 281-295.
Haddad, N. M., L. A. Brudvig, J. Clobert, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1(2): e1500052.
Hansen, M. C., P. V. Potapov, R. Moore, et al. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342(6160): 850-853.
Hansen, M. C., S. V. Stehman, P. V. Potapov, et al. 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. Proceedings of the National Academy of Sciences of the United States of America 105(27): 9439-9444.
Harmsen, B. J., R. J. Foster, S. Silver, L. Ostro, and C. P. Doncaster. 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. Biotropica 42(1): 126-133.
Harrison, R. L. 1992. Toward a theory of inter-refuge corridor design. Conservation Biology 6(2): 293-295.
Harvey, C. A. 2000. Colonization of agricultural windbreaks by forest trees: Effects of connectivity and remnant trees. Ecological Applications 10(6): 1762-1773.
Hatanaka, M., C. Bain, and L. Busch. 2005. Third-party certification in the global agrifood system. Food policy 30(3): 354-369.
Hausmann, F., C. P. Catterall, and S. D. Piper. 2005. Effects of edge habitat and nest characteristics on depredation of artificial nests in fragmented Australian tropical rainforest. Biodiversity and Conservation 14(10): 2331-2345.
Hawes, J., J. Barlow, T. A. Gardner, and C. A. Peres. 2008. The value of forest strips for understorey birds in an Amazonian plantation landscape. Biological Conservation 141(9): 2262-2278.
HCVRN. 2013. Common guidance for the identification of High Conservation Values. HCV Resource Network.

Hellier, A., A. C. Newton, and S. O. Gaona. 1999. Use of indigenous knowledge for rapidly assessing trends in biodiversity: a case study from Chiapas, Mexico. Biodiversity & Conservation 8(7): 869-889.
Henderson, A., G. Galeano-Garces, and R. Bernal. 1997. Field guide to the palms of the Americas. Princeton University Press.
Hess, G. R. 1994. Conservation corridors and contagious disease: A cautionary note. Conservation Biology 8(1): 256-262.
Hess, G. R., and R. A. Fischer. 2001. Communicating clearly about conservation corridors. Landscape and Urban Planning 55(3): 195-208.
Hietz-Seifert, U., P. Hietz, and S. Guevara. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biological Conservation 75(2): 103-111.
Hill, C. J. 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. Conservation Biology 9(6): 1559-1566.
Hilty, J. A., W. Z. Lidicker Jr., and A. M. Merenlender. 2006. Corridor Ecology: The science and practice of linking landscapes for biodiversity conservation. Island Press, Washington, D.C.
Holmes, D. A. 2002. Indonesia: Where have all the forests gone? Environmental and Social Development Unit, The World Bank, East Asia and Pacific Region.
Horskins, K., P. B. Mather, and J. C. Wilson. 2006. Corridors and connectivity: when use and function do not equate. Landscape Ecology 21(5): 641-655.
Hsieh, T., K. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7(12): 1451-1456.
Hsieh, T. C., K. H. Ma, and A. Chao. 2013. iNEXT online: interpolation and extrapolation (Version 1.3.0) http://chao.stat.nthu.edu.tw/blog/softwaredownload/.
Ibarra-Macias, A., W. D. Robinson, and M. S. Gaines. 2011a. Experimental evaluation of bird movements in a fragmented Neotropical landscape. Biological Conservation 144(2): 703-712.
Ibarra-Macias, A., W. D. Robinson, and M. S. Gaines. 2011b. Forest corridors facilitate movement of tropical forest birds after experimental translocations in a fragmented Neotropical landscape in Mexico. Journal of Tropical Ecology 27(5): 547-556.
International Union for Conservation of Nature [IUCN]. 2016. The IUCN Red List of Threatened Species.http://www.iucnredlist.org/.
ISI. 2017. Web of Science. Web of Knowledge, Thomson Reuters. Retreived May 2017 from https://www.webofknowledge.com/
Jain, A., K. Chong, M. Chua, and G. Clements. 2014. Moving away from paper corridors in Southeast Asia. . Conservation Biology 28(4): 889-891.
Jesus, F. M., V. R. Pivello, S. T. Meirelles, G. Franco, and J. P. Metzger. 2012. The importance of landscape structure for seed dispersal in rain forest fragments. Journal of Vegetation Science 23(6): 1126-1136.
Jiménez, G. 2001. Propuesta metodológica para el diseño y validación de corredores biológicos en Costa Rica. Proposal of a method to design and validate biological corridors in Costa Rica. Revista Forestal Centroamericana.(34): 73-79.
Jimenez, J. J. 2012. Personal communication.
Johnsingh, A. J. T., S. N. Prasad, and S. P. Goyal. 1990. Conservation status of the Chila-Motichur Corridor for elephant movement in Rajaji-Corbett National Parks area, India. Biological Conservation 51(2): 125-138.
Johnsingh, A. J. T., and A. C. Williams. 1999. Elephant corridors in India: lessons for other elephant range countries. Oryx 33(3): 210-214.
Jolliffe, B. 2006. Getting Connected Out On The Osa. Critical Ecosystem Partnership Fund http://www.cepf.net/news/top_stories/Pages/apr302006_connected_osa.aspx.

Jones, D. L. 1995. Palms Throughout the World. Smithsonian Institution Press. USA.
Jordan, C. A., K. J. Stevens, G. R. Urquhart, D. B. Kramer, and K. Roe. 2010. A new record of Baird's tapir *Tapirus bairdii* in Nicaragua and potential implications. Tapir Conservation Newsletter 19(1): 11-15.
Kanowski, J. J., T. M. Reis, C. P. Catterall, and S. D. Piper. 2006. Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. Restoration Ecology 14(1): 67-76.
Kappelle, M., M. Castro, H. Acevado, L. Gonzalez, and H. Monge. 2003. Ecosystems of the Osa Conservation Area (ACOSA). Instituto Nacional de Biodiversidad (INBio), Costa Rica.
Karanth, K. U., and M. E. Sunquist. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Journal of Zoology 250(02): 255-265.
Keeley, A. T., P. Beier, B. W. Keeley, and M. E. Fagan. 2017. Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landscape and Urban Planning 161: 90-102.
Kelly, M. J. 2008. Design, evaluate, refine: camera trap studies for elusive species. Animal Conservation 11(3): 182-184.
Keuroghlian, A., A. Desbiez, R. Reyna-Hurtado, M. Altrichter, H. Beck, A. Taber, and J. M. V. Fragoso. 2013. Tayassu pecari. The IUCN Red List of Threatened Species 2013 http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T41778A44051115.en.
Kikoti, A. P., C. R. Griffin, and L. Pamphil. 2010. Elephant use and conflict leads to Tanzania's first wildlife conservation corridor. Pachyderm(48): 57-66.
KKI Warsi, FZS, Eyes on the Forest, and WWF-Indonesia. 2010. *Last Chance to Save Bukit Tigapuluh: Sumatran tigers, elephants, orangutans and indigenous tribes face local extinction, along with forest*. KKI Warsi, Frankfurt Zoological Society, Eyes on the Forest, & WWF - Indonesia, Indonesia.
Knowlton, J. L., C. C. Phifer, P. V. Cerqueira, et al. 2017. Oil Palm Plantations Affect Movement Behavior of a Key Member of Mixed-Species Flocks of Forest Birds in Amazonia, Brazil. Tropical Conservation Science 10: 1940082917692800.
Koh, L. P., P. Levang, and J. Ghazoul. 2009. Designer landscapes for sustainable biofuels. Trends in Ecology & Evolution 24(8): 431-438.
Koh, L. P., and D. S. Wilcove. 2008. Is oil palm agriculture really destroying tropical biodiversity? Conservation Letters 1(2): 60-64.
Kormann, U., C. Scherber, T. Tscharntke, N. Klein, M. Larbig, J. J. Valente, A. S. Hadley, and M. G. Betts. 2016. Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. Proceedings of the Royal Society B-Biological Sciences 283(1823): 20152347.
Krewenka, K. M., A. Holzschuh, T. Tscharntke, and C. F. Dormann. 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. Biological Conservation 144(6): 1816-1825.
Krosby, M., I. Breckheimer, D. John Pierce, et al. 2015. Focal species and landscape "naturalness" corridor models offer complementary approaches for connectivity conservation planning. Landscape Ecology 30(10): 2121-2132.
Landmann, A., C. Walder, A. Vorauer, and T. Emser. 2008. Mammals of the Piedras Blancas National Park, Costa Rica: species composition, habitat associations and efficiency of research methods–a preliminary overview. Stapfia 80: 409-422.
LaPoint, S., P. Gallery, M. Wikelski, and R. Kays. 2013. Animal behavior, cost-based corridor models, and real corridors. Landscape Ecology 28(8): 1615-1630.
Laurance, S. G., and W. F. Laurance. 1999. Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. Biological Conservation 91(2-3): 231-239.
Laurance, S. G. W. 2004. Landscape connectivity and biological corridors. Pages 50–63 *in* G. A. Schroth, B. Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, and A. M. N. Izac,

editors. Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, DC.
Laurance, W. F. 1990. Comparative Responses of 5 Arboreal Marsupials to Tropical Forest Fragmentation. Journal of Mammalogy 71(4): 641-653.
Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5(1): 79-89.
Laurance, W. F. 1999. Reflections on the tropical deforestation crisis. Biological Conservation 91(2-3): 109-117.
Laurance, W. F., J. L. Camargo, R. C. Luizão, et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biological Conservation 144(1): 56-67.
Laurance, W. F., L. P. Koh, R. Butler, N. S. Sodhi, C. J. Bradshaw, J. D. Neidel, H. Consunji, and J. Mateo Vega. 2010. Improving the performance of the Roundtable on Sustainable Palm Oil for nature conservation. Conservation Biology 24(2): 377-381.
Laurance, W. F., S. G. Laurance, and D. W. Hilbert. 2008. Long-Term Dynamics of a Fragmented Rainforest Mammal Assemblage. Conservation Biology 22(5): 1154-1164.
Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, et al. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16(3): 605-618.
Lechner, A. M., D. Sprod, O. Carter, and E. C. Lefroy. 2017. Characterising landscape connectivity for conservation planning using a dispersal guild approach. Landscape Ecology 32(1): 99-113.
Lees, A. C., and C. A. Peres. 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conservation Biology 22(2): 439-449.
Linden, D. W., A. K. Fuller, J. A. Royle, and M. P. Hare. 2017. Examining the occupancy–density relationship for a low-density carnivore. Journal of Applied Ecology 54(6): 2043-2052.
Lindenmayer, D., J. Franklin, and J. Fischer. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131(3): 433-445.
Lindenmayer, D. B., and H. A. Nix. 1993. Ecological principles for the design of wildlife corridors. Conservation Biology 7(3): 627-630.
Linkie, M., Y. Dinata, A. Nugroho, and I. A. Haidir. 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation 137(1): 20-27.
Linkie, M., G. Guillera-Arroita, J. Smith, et al. 2013. Conserving cryptic mammals on camera: assessing the utility of range wide camera trap data for conserving the endangered Asian tapir. Biological Conservation 162: 107-115.
Lynam, A. J., S. T. Khaing, and K. M. Zaw. 2006. Developing a national tiger action plan for the union of Myanmar. Environmental Management 37(1): 30-39.
MacKenzie, D., J. Royle, J. Brown, and J. Nichols. 2004. Occupancy estimation and modeling for rare and elusive populations. Pages 149–172 *in* W. L. Thompson, editor. Sampling Rare or Elusive Species Concepts Designs and Techniques for Estimating Population Parameters. Island Press, Washington, DC.
MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83(8): 2248-2255.
Maddox, T., D. Priatna, E. Gemita, and A. Salampessy. 2007. The conservation of tigers and other wildlife in oil palm plantations. Jambi Province, Sumatra, Indonesia. The Zoological Society of London, London, England.
Martensen, A. C., R. G. Pimentel, and J. P. Metzger. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. Biological Conservation 141(9): 2184-2192.

Martin, E. A., M. Viano, L. Ratsimisetra, F. Laloe, and S. M. Carriere. 2012. Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. Agriculture Ecosystems & Environment 149: 1-9.
McCarthy, J., and Z. Zen. 2010. Regulating the oil palm boom: Assessing the effectiveness of environmental governance approaches to agro‐industrial pollution in Indonesia. Law & Policy 32(1): 153-179.
McClure, C. J. W., B. W. Rolek, and G. E. Hill. 2012. Predicting occupancy of wintering migratory birds: Is microhabitat information necessary? Condor 114: 482–490.
McKelvey, K. S., K. B. Aubry, and M. K. Schwartz. 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. BioScience 58(6): 549-555.
McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89(10): 2712-2724.
McRae, B. H., and D. M. Kavanagh. 2017. Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle, WA. 2011.
McRae, B. H., V. B. Shah, and T. Mohapatra. 2014. Circuitscape v4.0. The Nature Conservancy, Seattle, WA.
McShea, W. J. 2014. What are the roles of species distribution models in conservation planning? Environmental Conservation 41(02): 93-96.
McShea, W. J., C. Stewart, L. Peterson, P. Erb, R. Stuebing, and B. Giman. 2009. The importance of secondary forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. Biological Conservation 142(12): 3108-3119.
Meisel, J. E. 2006. Thermal ecology of the neotropical army ant Eciton burchellii. Ecological Applications 16(3): 913-922.
Metzger, J. P. 1997. Relationships between landscape structure and tree species diversity in tropical forests of South-East Brazil. Landscape and Urban Planning 37(1-2): 29-35.
Metzger, J. P., L. C. Bernacci, and R. Goldenberg. 1997. Pattern of tree species diversity in riparian forest fragments of different widths (SE Brazil). Plant Ecology 133(2): 135-152.
Metzger, J. P., A. C. Martensen, M. Dixo, L. C. Bernacci, M. C. Ribeiro, A. M. G. Teixeira, and R. Pardini. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142(6): 1166-1177.
Miettinen, J., C. Shi, and S. C. Liew. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17(7): 2261-2270.
Munoz, J. C., R. Aerts, K. W. Thijs, P. R. Stevenson, B. Muys, and C. H. Sekercioglu. 2013. Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland. Agriculture Ecosystems & Environment 173: 13-19.
Murdiyarso, D., S. Dewi, D. Lawrence, and F. Seymour. 2011. Indonesia's forest moratorium: A stepping stone to better forest governance? CIFOR, Bogor, Indonesia.
Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772): 853-858.
Naranjo, E. J. 2009. Ecology and conservation of Baird's tapir in Mexico. Tropical Conservation Science 2(2): 140-158.
Nasi, R., and P. Frost. 2009. Sustainable forest management in the tropics: is everything in order but the patient still dying? Ecology and Society 14(2): 40.
Nasi, R., P. Koponen, J. G. Poulsen, M. Buitenzorgy, and W. Rusmantoro. 2008. Impact of landscape and corridor design on primates in a large-scale industrial tropical plantation landscape. Biodiversity and Conservation 17(5): 1105-1126.
Newmark, W. D., V. J. Mkongewa, and A. D. Sobek. 2010. Ranging behavior and habitat selection of terrestrial insectivorous birds in north-east Tanzania: implications for corridor design in the Eastern Arc Mountains. Animal Conservation 13(5): 474-482.

O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono. 2003a. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6: 131-139.
O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono. 2003b. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6(02): 131-139.
O'Connell, A. F., J. D. Nichols, and K. U. Karanth, editors. 2011. Camera Traps in Animal Ecology: Methods and Analysis. Springer, Tokyo.
Obando, V., and H. Acevedo. 2007. Propuesta de límites para el Corredor Biológico Osa (CBO) basados en criterios científico-biológicos y de acuerdo con los objetos de conservación prioritarios [Proposal of limits for the Osa Biological Corridor (CBO) based on scientific-biological criteria and in accordance with priority conservation objectives]. National Biodiversity Institute of Costa Rica, Santo Domingo de Heredia, Costa Rica.
Obidzinski, K., and A. Dermawan. 2012. Pulp industry and environment in Indonesia: is there sustainable future? Regional Environmental Change 12(4): 961-966.
Olson, D. M., E. Dinerstein, E. D. Wikramanayake, et al. 2001. Terrestrial ecoregions of the worlds: a new map of life on Earth. BioScience 51(11): 933-938.
Olson, G. S., R. G. Anthony, E. D. Forsman, S. H. Ackers, P. J. Loschl, J. A. Reid, K. M. Dugger, E. M. Glenn, and W. J. Ripple. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. Journal of Wildlife Management 69(3): 918–932.
Paetkau, D., E. Vázquez‐Domínguez, N. I. Tucker, and C. Moritz. 2009. Monitoring movement into and through a newly planted rainforest corridor using genetic analysis of natal origin. Ecological management & restoration 10(3): 210-216.
Pagiola, S. 2008. Payments for environmental services in Costa Rica. Ecological economics 65(4): 712-724.
Panthera. 2012. Panthera's Tiger Corridor Work in Sumatra, Indonesia.http://www.panthera.org/programs/tiger/tiger-corridor-initiative/sumatra-indonesia.
Paoli, G. D., P. Gillespie, P. L. Wells, L. Hovani, A. Sileuw, N. Franklin, and J. Schweithelm. 2013. Oil palm in Indonesia: Governance, decision making and implications for sustainable development. The Nature Conservancy Indonesia Program, Jakarta, Indonesia.
Paolucci, L. N., R. R. C. Solar, T. G. Sobrinho, C. F. Sperber, and J. H. Schoereder. 2012. How does small-scale fragmentation affect litter-dwelling ants? The role of isolation. Biodiversity and Conservation 21(12): 3095-3105.
Pardini, R., S. M. de Souza, R. Braga-Neto, and J. P. Metzger. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biological Conservation 124(2): 253-266.
Parren, M. P. E., B. M. de Leede, and F. Bongers. 2002. A proposal for a transnational forest network area for elephants in Cote d'Ivoire and Ghana. Oryx 36(3): 249-256.
Phalan, B., E. B. Fitzherbert, S. Rafflegeau, M. J. Struebig, and A. Verwilghen. 2009. Conservation in oil-palm landscapes. Conservation Biology 23(2): 244-245.
Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344(6187): 1246752.
Pirker, J., A. Mosnier, F. Kraxner, P. Havlík, and M. Obersteiner. 2016. What are the limits to oil palm expansion? Global Environmental Change 40: 73-81.
Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.*in* Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria.
Plumptre, A. J. 2000. Monitoring mammal populations with line transect techniques in African forests. Journal of Applied Ecology 37(2): 356-368.

Polisar, J., I. Maxit, D. Scognamillo, L. Farrell, M. E. Sunquist, and J. F. Eisenberg. 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biological Conservation 109(2): 297-310.
Powell, A., A. Rylands, C. Quintela, et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soulé, editor. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, University of Minnesota.
Procheş, Ş., J. R. Wilson, R. Veldtman, J. M. Kalwij, D. M. Richardson, and S. L. Chown. 2005. Landscape corridors: possible dangers? Science 310(5749): 779-783.
ProForest. 2006. HCVF assessment of two concessions in Teso Nilo: Findings and management recommendations. ProForest Ltd., Oxford, UK.
R Development Core Team. 2014. R. R Project for Statistical Computing, Vienna, Austria.
R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rabinowitz, A., and K. A. Zeller. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biological Conservation 143(4): 939-945.
Ramiadantsoa, T., O. Ovaskainen, J. Rybicki, and I. Hanski. 2015. Large-Scale Habitat Corridors for Biodiversity Conservation: A Forest Corridor in Madagascar. PLoS ONE 10(7): e0132126.
Reid, F. 1997. A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press.
Reilly, M. L., M. W. Tobler, D. L. Sonderegger, and P. Beier. 2017. Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. Biological Conservation 207: 117-126.
Republic of Indonesia. 2011. Peraturan Pemerintah Republik Indonesia Nomor 38 Tahun 2011 tentang Sungai [Indonesian Government Regulation No. 38 Year 2011 about Rivers]. Pages Pasal 10, Ayat 11 [Article 10, Paragraph 11]. Government of the Republic of Indonesia, Jakarta, Indonesia.
Rich, L. N., D. A. W. Miller, H. S. Robinson, J. W. McNutt, and M. J. Kelly. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. Journal of Applied Ecology 53(4): 1225-1235.
Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist 158(1): 87-99.
Riitters, K., J. Wickham, J. K. Costanza, and P. Vogt. 2016. A global evaluation of forest interior area dynamics using tree cover data from 2000 to 2012. Landscape Ecology 31(1): 137-148.
Rocha, M. F., M. Passamani, and J. Louzada. 2011. A small mammal community in a forest fragment, vegetation corridor and coffee matrix system in the Brazilian Atlantic Forest. PLoS ONE 6(8): e23312.
Rouget, M., R. M. Cowling, A. T. Lombard, A. T. Knight, and I. H. K. Graham. 2006. Designing large-scale conservation corridors for pattern and process. Conservation Biology 20(2): 549-561.
Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84(3): 777-790.
RSPO. 2013. Principles and Criteria for Sustainable Palm Oil Production. Roundtable on Sustainable Palm Oil, Kuala Lumpur, Malaysia.
RSPO. 2016. Impact.http://www.rspo.org/about/impacts.
Saladero Ecolodge. 2017. Golfo Dulce-Piedras Blancas National Park, Costa Rica http://www.saladeroecolodge.com/national-park.
Salom-Pérez, R., E. Carrillo, J. C. Sáenz, and J. M. Mora. 2007. Critical condition of the jaguar Panthera onca population in Corcovado National Park, Costa Rica. Oryx 41(01): 51-56.
Sayer, J., J. Ghazoul, P. Nelson, and A. K. Boedhihartono. 2012. Oil palm expansion transforms tropical landscapes and livelihoods. Global Food Security 1(2): 114-119.

Seaman, B. S., and C. H. Schulze. 2010. The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. Biological Conservation 143(2): 391-398.
Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology 1(1): 63-71.
Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors - Conservation bargains or poor investments? Conservation Biology 6(4): 493-504.
Sodhi, N. S., C. Briffett, L. Kong, and B. Yuen. 1999. Bird use of linear areas of a tropical city: implications for park connector design and management. Landscape and Urban Planning 45(2-3): 123-130.
Sollmann, R., M. M. Furtado, B. Gardner, H. Hofer, A. T. Jácomo, N. M. Tôrres, and L. Silveira. 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. Biological Conservation 144(3): 1017-1024.
Sollmann, R., M. M. Furtado, H. Hofer, A. T. A. Jácomo, N. M. Tôrres, and L. Silveira. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammailian Biology-Zeitschrift für Säugetierkunde, 77(1): 41-46.
Sollmann, R., A. Mohamed, J. Niedballa, et al. 2017. Quantifying mammal biodiversity co-benefits in certified tropical forests. Diversity and Distributions 23(3): 317-328.
Stewart, A.-M. E., C. H. Gordon, and E. Meijaard. 2007. Practitioners guide to rapid mammal surveys as a tool for HCVF assessments in Borneo: A guide applicable to tropical rainforests in South-East Asia. The Nature Conservancy, Samarinda, Indonesia.
Stewart, C., P. George, T. Rayden, and R. Nussbaum. 2008. Good practice guidelines for High Conservation Value assessments. ProForest: Oxford, UK.
Struebig, M. J., G. Paoli, and E. Meijaard. 2010. A reality check for designer biofuel landscapes. Trends in Ecology & Evolution 25(1): 7-8.
Sunarto, S., M. J. Kelly, K. Parakkasi, S. Klenzendorf, E. Septayuda, and H. Kurniawan. 2012. Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. PLoS ONE 7(1): e30859.
Thier, O., and J. Wesenberg. 2016. Floristic composition and edge-induced homogenization in tree communities in the fragmented Atlantic rainforest of Rio de Janeiro, Brazil. Tropical Conservation Science 9(2): 852-876.
Thomas, B., J. D. Holland, and E. O. Minot. 2008. Elephant (*Loxodonta africana*) home ranges in Sabi Sand Reserve and Kruger National Park: A five-year satellite tracking study. PLoS ONE 3(12): e3902.
Tobler, M. W., S. E. Carrillo-Percastegui, R. Leite Pitman, R. Mares, and G. Powell. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Animal Conservation 11(3): 169-178.
Tobler, M. W., S. E. Carrillo-Percastegui, and G. Powell. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. Journal of Tropical Ecology 25(03): 261-270.
Tobler, M. W., A. Zúñiga Hartley, S. E. Carrillo-Percastegui, and G. V. Powell. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. Journal of Applied Ecology 52(2): 413-421.
Trainor, A. M., J. R. Walters, W. F. Morris, J. Sexton, and A. Moody. 2013. Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers. Landscape Ecology 28(4): 755-767.
Tucker, M. A., K. Böhning-Gaese, W. F. Fagan, et al. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359(6374): 466-469.

Uezu, A., D. D. Beyer, and J. P. Metzger. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? Biodiversity and Conservation 17(8): 1907-1922.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123(4): 507-519.

United States Department of Agriculture [USDA]. 2004. Conservation Corridor Planning at the Landscape Level—Managing for Wildlife Habitat. Pages 1-130 National Biology Handbook. Natural Resources Conservation Service of the United States Department of Agriculture, Washington, DC.

Vieira, F. D., and D. de Carvalho. 2008. Genetic structure of an insect-pollinated and bird-dispersed tropical tree in vegetation fragments and corridors: implications for conservation. Biodiversity and Conservation 17(10): 2305-2321.

Volpe, N. L., W. D. Robinson, S. J. K. Frey, A. S. Hadley, and M. G. Betts. 2016. Tropical Forest Fragmentation Limits Movements, but Not Occurrence of a Generalist Pollinator Species. PLoS ONE 11(12): e0167513.

Wainwright, M. 2007. The Mammals of Costa Rica: A Natural History and Field Guide. Cornell University Press, New York, USA

Walker, R. 2004. *Conepatus semistriatus*. Animal Diversity Web.

Wang, F., W. J. McShea, D. Wang, S. Li, Q. Zhao, H. Wang, and Z. Lu. 2014. Evaluating landscape options for corridor restoration between giant panda reserves. PLoS ONE 9(8): e105086.

Weinbaum, K., Z. Nzooh, L. Usongo, and M. Laituri. 2007. Preliminary survey of forest elephant crossings in Sangha Trinational Park, central Africa. Pachyderm(43): 52-62.

Wilson, D. E. 1983. Mammals. Page 496 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press.

Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages pp. 522–534 *in* M. L. Cody and J. M. Diamond, editors. Ecology and Evolution of Communities. Belknap Pres, Cambridge, Massachusetts.

Wilson, K. A., E. Meijaard, S. Drummond, et al. 2010. Conserving biodiversity in production landscapes. Ecological Applications 20(6): 1721-1732.

WWF. 2006. The Eleventh Hour for Riau's Forests: Two global pulp and paper companies will decide their fate. World Wide Fund for Nature, Jakarta, Indonesia.

Yaap, B., A. Magrach, G. R. Clements, C. J. W. McClure, G. D. Paoli, and W. F. Laurance. 2016. Large Mammal Use of Linear Remnant Forests in an Industrial Pulpwood Plantation in Sumatra, Indonesia. Tropical Conservation Science 9(4): 13.

Yaap, B., M. J. Struebig, G. Paoli, and L. P. Koh. 2010. Mitigating the biodiversity impacts of oil palm development. CAB Reviews 5(19): 1-11.

Yamaura, Y., J. A. Royle, N. Shimada, S. Asanuma, T. Sato, H. Taki, and S. i. Makino. 2012. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodiversity and Conservation 21(6): 1365-1380.

Yu, J., and F. S. Dobson. 2000. Seven forms of rarity in mammals. Journal of Biogeography 27(1): 131-139.

Yumnam, B., Y. V. Jhala, Q. Qureshi, J. E. Maldonado, R. Gopal, S. Saini, Y. Srinivas, and R. C. Fleischer. 2014. Prioritizing Tiger Conservation through Landscape Genetics and Habitat Linkages. PLoS ONE 9(11): e111207.

Zeller, K. 2016. Evaluating resistance surfaces for modeling wildlife movement and connectivity. University of Massachusetts, Amherst, Massachusetts, USA.

Zeller, K. A., K. McGarigal, S. A. Cushman, P. Beier, T. W. Vickers, and W. M. Boyce. 2016. Using step and path selection functions for estimating resistance to movement: pumas as a case study. Landscape Ecology 31(6): 1319-1335.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27(6): 777-797.
Zeller, K. A., S. Nijhawan, R. Salom-Pérez, S. H. Potosme, and J. E. Hines. 2011. Integrating occupancy modeling and interview data for corridor identification: A case study for jaguars in Nicaragua. Biological Conservation 144(2): 892-901.
Zimbres, B., C. A. Peres, and R. B. Machado. 2017. Terrestrial mammal responses to habitat structure and quality of remnant riparian forests in an Amazonian cattle-ranching landscape. Biological Conservation 206: 283-292.

Appendix A. Papers included in literature review

Author(s)	Year	Taxa	Landscape: Experimental (EXP) - Observational (OBS)	Variable: Demographic (DEM) or pure movement (MOV)	Approach: Genetic (GEN), Radio telemetry (RAD), Mark-recapture (MRC), Occupancy (OCC)	Country
Powell et al.	1986	Birds	OBS	DEM + MOV	OCC	Brazil (Amazon)
Laurance*	1990	Mammal (arboreal)	OBS	DEM	OCC	Australia (Atherton Tablelands)
Laurance*	1991	Mammals (non-volant)	OBS	DEM	OCC	Australia (Atherton Tablelands)
Hill*	1995	Invertebrates (ant, dung beetle, butterfly)	OBS	DEM	OCC	Australia (North QLD)
Hietz-Seifert et al.	1996	Plant (epiphytes)	OBS	DEM	OCC	Mexico
Metzger	1997	Plants (trees)	OBS	DEM	OCC	Brazil (SE)
Metzger et al.	1997	Plants (trees)	OBS	DEM	OCC	Brazil (SE)
de Lima and Gascon*	1999	Mammal (small) & frogs	OBS	DEM	OCC	Brazil (Amazon)
Johnsingh and Williams	1999	Mammal (elephant)	OBS	DEM	OCC	India
Laurance and Laurance	1999	Mammal (arboreal)	OBS	DEM	OCC	Australia (Atherton Tablelands)
Sodhi et al.*	1999	Birds	OBS	DEM	OCC	Singapore
Estrada et al.	2000	Birds	OBS	DEM	OCC	Mexico
Harvey	2000	Plants (trees)	OBS	DEM	OCC	Costa Rica
Estrada and Coates-Estrada	2001	Mammal (bat)	OBS	DEM	OCC	Mexico

Author(s)	Year	Taxa	Landscape: Experimental (EXP) - Observational (OBS)	Variable: Demographic (DEM) or pure movement (MOV)	Approach: Genetic (GEN), Radio telemetry (RAD), Mark-recapture (MRC), Occupancy (OCC)	Country
Estrada and Coates-Estrada	2001	Mammal (bat)	OBS	DEM	OCC	Mexico
Parren et al.*	2002	Mammal (elephant)	OBS	DEM	OCC	Ghana/Cote d'Ivore
Hausmann et al.*	2005	Birds	OBS	DEM	OCC	Australia (Atherton Tablelands)
Pardini et al.	2005	Mammal (small)	OBS	DEM	OCC	Brazil (Atlantic forest)
Uezu et al.*	2005	Birds	OBS	DEM	OCC	Brazil (Atlantic Forest)
Horskins et al.	2006	Mammal (rats)	OBS	DEM	GEN	Australia (Atherton Tablelands)
Kanowski et al.	2006	Reptiles (lizards and snakes)	OBS	DEM	OCC	Australia (Atherton Tablelands)
Meisel	2006	Invertebrates (ants)	EXP	MOV	OCC	Costa Rica
Weinbaum et al.	2007	Mammal (elephant)	OBS	DEM	OCC	Central Africa
Hawes et al.	2008	Birds	OBS	DEM	OCC	Brazil (Amazon)
Laurance et al.	2008	Mammal (arboreal)	OBS	DEM	OCC	Australia (Atherton Tablelands)
Lees and Peres	2008	Mammals (large) & birds	OBS	DEM	OCC	Brazil (Amazon)
Martensen et al.	2008	Birds	OBS	DEM	OCC	Brazil (Atlantic Forest)
Nasi et al.	2008	Mammal (primate)	OBS	DEM	OCC	Indonesia (Sumatra)
Uezu et al.*	2008	Birds	OBS	DEM	OCC	Brazil (Atlantic Forest)
Vieira and de Carvalho	2008	Plants (trees)	OBS	DEM	GEN	Brazil (Minas Gerais)
Dixo et al.	2009	Amphibian (toad)	OBS	DEM	GEN	Brazil (Atlantic Forest)
McShea et al.*	2009	Mammal (large)	OBS	DEM	OCC	Malaysia

Author(s)	Year	Taxa	Landscape: Experimental (EXP) - Observational (OBS)	Variable: Demographic (DEM) or pure movement (MOV)	Approach: Genetic (GEN), Radio telemetry (RAD), Mark-recapture (MRC), Occupancy (OCC)	Country
Metzger et al.	2009	Mammal (small), birds, frogs & trees	OBS	DEM	OCC	Brazil (Atlantic Forest)
Paetkau et al.	2009	Mammal (rats)	OBS + EXP	DEM + MOV	GEN	Australia (Atherton Tablelands)
Barlow et al.	2010	Mammals (large) & dung beetles	OBS	DEM	OCC	Brazil (Amazon)
Diaz-Gallegos et al.*	2010	Invertebrate (dung and carrion beetles)	OBS	DEM	OCC	Mexico
Gillies and St. Clair	2010	Birds	OBS	MOV	RAD	Costa Rica
Seaman and Schulze	2010	Birds	OBS	DEM	OCC	Costa Rica
Galanes and Thomlinson	2011	Invertebrates (millipedes)	OBS	DEM	OCC	Puerto Rico
Gillies et al.	2011	Birds	OBS	MOV	RAD	Costa Rica
Ibarra-Macias et al.	2011	Birds	OBS	MOV	MRC	Mexico
Rocha et al. *	2011	Mammal (small)	OBS	DEM	OCC	Brazil (Atlantic Forest)
Jesus et al.	2012	Plants (trees)	OBS	DEM	OCC	Brazil (Atlantic forest)
Martin et al.	2012	Birds	OBS	DEM	OCC	Madagascar
Paolucci et al.	2012	Invertebrates (ants)	EXP	DEM	OCC	Brazil (Atlantic Forest)
Gould et al.	2013	Invertebrates (wasps)	OBS	DEM	OCC	Hawaii
Munoz et al.	2013	Birds & trees	OBS	DEM	OCC	Columbia
Gray et al.	2014	Invertebrates (dung beetles)	OBS	DEM	OCC	Malaysia

Author(s)	Year	Taxa	Landscape: Experimental (EXP) - Observational (OBS)	Variable: Demographic (DEM) or pure movement (MOV)	Approach: Genetic (GEN), Radio telemetry (RAD), Mark-recapture (MRC), Occupancy (OCC)	Country
de la Pena-Cuellar et al.	2015	Mammal (bat)	OBS	DEM	OCC	Mexico
Ramiadantsoa et al.	2015	Mammal (lemurs & small), bird, amph & reptiles	OBS	DEM	OCC	Madagascar
Almeida et al.	2016	Birds	OBS	DEM	OCC	Brazil (Amazon)
Gray et al.	2016	Invertebrates (dung beetles and ants)	OBS	DEM	OCC	Malaysia
Kormann et al.	2016	Birds	OBS + EXP	MOV + DEM	OCC	Costa Rica
Volpe et al.	2016	Birds	OBS	MOV	RAD	Costa Rica
Yaap et al.	2016	Mammal (large)	OBS	DEM	OCC	Indonesia (Sumatra)
Zimbres et al.	2016	Mammal (large)	OBS	DEM	OCC	Brazil (Amazon)
Costa et al.	2017	Invertebrates (dung beetles)	OBS	DEM	OCC	Brazil (Minas Gerais)
Knowlton et al.	2017	Birds	OBS	MOV	RAD	Brazil (Amazon)

* Study not identified in the initial ISI Web of Science search, but identified through work cited in other studies or on Google Scholar.

Appendix B. Species list from specific studies in the literature review

Corridor use by species in Lees and Peres (2008)

Species	Scientific name	Control	Connected corridor	Unconnected corridor
Small armadillo	*Dasypus spp.*	Present	Present	Present
Capybara	*Hydrochoerus hydrochaeris*	Less frequently than corridors	Present	Present
Paca	*Paca agouti*	Common	Common	Rarer
White-lipped peccaries	*Tayassu pecari*	Present	Present	Absent
Tapir	*Tapirus terrestris*	Not explicitly stated in text, but assumed present	Not explicitly stated in text, but assumed present	Present (matrix tolerant)
Collared peccaries	*Pecari tajacu*	Not explicitly stated in text, but assumed present	Not explicitly stated in text, but assumed present	Present (matrix tolerant)
Brown capuchins	*Cebus apella*	Not explicitly stated in text, but assumed present	Not explicitly stated in text, but assumed present	Present (matrix tolerant)
Dusky titi-monkeys	*Callicebus moloch*	Not explicitly stated in text, but assumed present	Not explicitly stated in text, but assumed present	Present (matrix tolerant)
Spider monkey	*Ateles sp.*	Present	Absent	Absent
Tayras	*Eira barbara*	Equal frequency	Equal frequency	Equal frequency
Small cats	*Leopardus sp.*	Similar rate with connected	Similar rate with connected	Infrequently
	Puma yagouaroundi	Similar rate with connected	Similar rate with control	Infrequently
Large cats	*Puma concolor*	Regularly encountered	Uncommon	Rare
	Panthera onca	Regularly encountered	Uncommon	Rare

Note: Unfortunately, the paper did not provide a species list. The data in this table was extracted from the text.

Table taken directly from Barlow et al. (2010).

Species	Common name	Detection events
Cabassous unicinctus	Southern naked-tailed armadillo	355
Mazama americana	Red brocket deer	175
Dasyprocta agouti	Red-rumped agouti	93
Tapirus terrestris	Brazilian tapir	91
Dasypus spp.	Armadillo species	74
Saguinus midas midas	Golden-handed tamarin	58
Pecari tajacu	Collared peccary	50
Agouti paca	Paca	49
Mazama gouazoupira	Grey brocket deer	34
Panthera/puma	Large felid	29
Priodontes maximus	Giant armadillo	29
Cebus apella	Brown capuchin monkey	29
Myrmecophaga tridactyla	Giant anteater	28
Leopardus pardalis	Ocelot	23
Alouatta macconnelli	Guianan red howler monkey	21
Tayassu pecari	White-lipped peccary	19
Coendou prehensilis	Brazilian porcupine	8
Panthera onca	Jaguar	7
Puma concolor	Puma	3
Saimiri sciureus	Common squirrel monkey	3
Eira barbara	Tayra	2
Lontra longicaudis	Neotropical otter	2
Pithecia pithecia	Guianan saki monkey	2
Nasua nasua	South American coati	1
Speothos venaticus	Bush dog	1

Appendix C. Linear remnant study models

Table C1. Corridor-design and land-cover covariates (*psi* models) to identify the most important predictors of habitat use for species richness.

	K	AIC	Delta_AIC	AICWt	Cum.Wt	LL
DistMain	5	210.35	0	0.15	0.15	-100.17
AcOld+DistMain	6	210.35	0	0.15	0.3	-99.17
AcOld	5	210.37	0.02	0.15	0.44	-100.19
null	4	211.37	1.03	0.09	0.53	-101.69
DistMain+ConnMain	6	211.95	1.6	0.07	0.6	-99.97
AcYoung+ConnMain	6	212.09	1.74	0.06	0.66	-100.05
Dist+Main+Width	6	212.29	1.94	0.06	0.72	-100.14
Forest+DistMain	6	212.32	1.98	0.06	0.77	-100.16
Forest	5	212.63	2.28	0.05	0.82	-101.31
ConnMain	5	212.97	2.63	0.04	0.86	-101.49
Width	5	213.22	2.87	0.04	0.9	-101.61
AcOld	5	213.29	2.94	0.03	0.93	-101.65
Forest+ConnMain	6	214.19	3.84	0.02	0.95	-101.09
AcOld+ConnMain	6	214.46	4.11	0.02	0.97	-101.23
ConnMain+Width	6	214.81	4.46	0.02	0.99	-101.4
AcOld+Width	6	215.17	4.82	0.01	1	-101.58

Table C2. Detection probability models for eight species.

Tapir					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(IsoCorr)	212	0	0.8012	1	3
psi(.),p(.)	216.41	4.41	0.0883	0.1103	2
psi(.),p(season)	217.27	5.27	0.0575	0.0717	3
psi(.),p(bait)	218.32	6.32	0.034	0.0424	3
psi(.),p(corridor)	219.48	7.48	0.019	0.0238	5

Sun bear					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(.)	250.7	0	0.3108	1	2
psi(.),p(IsoCorr)	251.25	0.55	0.236	0.7596	3
psi(.),p(bait)	251.7	1	0.1885	0.6065	3
psi(.),p(corridor)	252.3	1.6	0.1396	0.4493	5
psi(.),p(season)	252.52	1.82	0.1251	0.4025	3

Pig-tailed macaque					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(IsoCorr)	263.98	0	0.5977	1	3
psi(.),p(corridor)	266.8	2.82	0.1459	0.2441	5
psi(.),p(.)	267.97	3.99	0.0813	0.136	2
psi(.),p(season)	268.1	4.12	0.0762	0.1275	3
psi(.),p(Setup)	268.44	4.46	0.0643	0.1075	3
psi(.),p(bait)	269.68	5.7	0.0346	0.0578	3

Wild pig					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(IsoCorr)	208.41	0	0.6406	1	3
psi(.),p(season)	210.77	2.36	0.1969	0.3073	3
psi(.),p(.)	212.45	4.04	0.085	0.1327	2
psi(.),p(bait)	214.18	5.77	0.0358	0.0559	3
psi(.),p(Setup)	214.44	6.03	0.0314	0.049	3
psi(.),p(corridor)	216.67	8.26	0.0103	0.0161	5

Mousedeer					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(corridor)	145.38	0	0.6971	1	5
psi(.),p(.)	149.31	3.93	0.0977	0.1402	2
psi(.),p(setup)	149.99	4.61	0.0695	0.0998	3
psi(.),p(season)	150.19	4.81	0.0629	0.0903	3
psi(.),p(bait)	151.26	5.88	0.0369	0.0529	3
psi(.),p(IsoCorr)	151.31	5.93	0.0359	0.0516	3

Malay porcupine					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(setup)	195.9	0	0.4604	1	3
psi(.),p(corridor)	197.52	1.62	0.2048	0.4449	5
psi(.),p(.)	198.63	2.73	0.1176	0.2554	2
psi(.),p(bait)	198.64	2.74	0.117	0.2541	3
psi(.),p(IsoCorr)	200.23	4.33	0.0528	0.1147	3
psi(.),p(season)	200.45	4.55	0.0473	0.1028	3

Red muntjac					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(setup)	219.84	0	0.7958	1	3
psi(.),p(.)	224.8	4.96	0.0666	0.0837	2
psi(.),p(IsoCorr)	224.85	5.01	0.065	0.0817	3
psi(.),p(bait)	226.66	6.82	0.0263	0.033	3
psi(.),p(season)	226.73	6.89	0.0254	0.0319	3
psi(.),p(corridor)	227.12	7.28	0.0209	0.0263	5

Malay civet					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(bait)	158.5	0	0.9937	1	3
psi(.),p(season)	169.81	11.31	0.0035	0.0035	3
psi(.),p(setup)	171.33	12.83	0.0016	0.0016	3
psi(.),p(.)	172.88	14.38	0.0007	0.0008	2
psi(.),p(IsoCorr)	174.46	15.96	0.0003	0.0003	3
psi(.),p(corridor)	176.1	17.6	0.0001	0.0002	5

Table C3. Occupancy models of habitat use for eight species using corridor-design and land-cover covariates (*psi* models) to identify the most important predictors of habitat use.

Tapir					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(Forest+DistMain),p(IsoCorr)	207.88	0	0.247	1	5
psi(Width+DistMain),p(IsoCorr)	207.98	0.1	0.235	0.9512	5
psi(DistMain),p(IsoCorr)	210.64	2.76	0.0622	0.2516	4
psi(Forest),p(IsoCorr)	210.89	3.01	0.0548	0.222	4
psi(ConnMain+DistMain),p(IsoCorr)	211	3.12	0.0519	0.2101	5
psi(Forest+ConnMain),p(IsoCorr)	211.03	3.15	0.0511	0.207	5
psi(ConnMain),p(IsoCorr)	211.31	3.43	0.0445	0.18	4
psi(Width+ConnMain),p(IsoCorr)	211.78	3.9	0.0351	0.1423	5
psi(.),p(IsoCorr)	212	4.12	0.0315	0.1275	3
psi(width),p(IsoCorr)	212.03	4.15	0.031	0.1256	4
psi(AcYoung),p(IsoCorr)	212.16	4.28	0.0291	0.1177	4
psi(AcOld+Width),p(IsoCorr)	212.37	4.49	0.0262	0.1059	5
psi(AcYoung+Width),p(IsoCorr)	212.53	4.65	0.0242	0.0978	5
psi(AcOld+DistMain),p(IsoCorr)	212.57	4.69	0.0237	0.0958	5
psi(AcOld+ConnMain),p(IsoCorr)	213.13	5.25	0.0179	0.0724	5
psi(AcOld),p(IsoCorr)	213.14	5.26	0.0178	0.0721	4
psi(AcYoung+ConnMain),p(IsoCorr)	213.23	5.35	0.017	0.0689	5

Sun bear					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(width),p(.)_GOF	248.44	0	0.1884	1	3
psi(Forest),p(.)	249.77	1.33	0.0969	0.5143	3
psi(AcOld+width),p(.)	249.83	1.39	0.094	0.4991	4
psi(DistMain+Width),p(.)	249.86	1.42	0.0926	0.4916	4
psi(AcYoung+width),p(.)	250.01	1.57	0.086	0.4561	4
psi(ConnMain+Width),p(.)	250.43	1.99	0.0697	0.3697	4
psi(.),p(.)	250.7	2.26	0.0609	0.323	2
psi(Forest+DistMain),p(.)	250.7	2.26	0.0609	0.323	4
psi(DistMain),p(.)	251.14	2.7	0.0489	0.2592	3
psi(Forest+ConnMain),p(.)	251.72	3.28	0.0366	0.194	4
psi(AcOld),p(.)	251.73	3.29	0.0364	0.193	3
psi(AcYoung),p(.)	252.43	3.99	0.0256	0.136	3
psi(ConnMain),p(.)	252.51	4.07	0.0246	0.1307	3
psi(DistMain+ConnMain),p(.)	252.78	4.34	0.0215	0.1142	4
psi(AcOld+DistMain),p(.)	252.92	4.48	0.0201	0.1065	4
psi(AcYoung+ConnMain),p(.)	252.95	4.51	0.0198	0.1049	4
psi(AcOld+ConnMain),p(.)	253.23	4.79	0.0172	0.0912	4

Pig-tailed macaque					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(IsoCorr)	263.98	0	0.1864	1	3
psi(AcYoung+width),p(IsoCorr)	265.67	1.69	0.0801	0.4296	5
psi(ConnMain),p(IsoCorr)	265.79	1.81	0.0754	0.4045	4
psi(DistMain),p(IsoCorr)	265.84	1.86	0.0735	0.3946	4
psi(forest+ConnMain),p(IsoCorr)	265.89	1.91	0.0717	0.3848	5
psi(AcYoung),p(IsoCorr)	265.97	1.99	0.0689	0.3697	4
psi(width),p(IsoCorr)	265.98	2	0.0686	0.3679	4
psi(AcOld),p(IsoCorr)	265.98	2	0.0686	0.3679	4
psi(forest),p(IsoCorr)	265.98	2	0.0686	0.3679	4
psi(ConnMain+width),p(IsoCorr)	267.04	3.06	0.0404	0.2165	5
psi(DistMain+ConnMain),p(IsoCorr)	267.52	3.54	0.0317	0.1703	5
psi(AcOld+ConnMain),p(IsoCorr)	267.56	3.58	0.0311	0.167	5
psi(AcYoung+ConnMain),p(IsoCorr)	267.79	3.81	0.0277	0.1488	5
psi(DistMain+width),p(IsoCorr)	267.81	3.83	0.0275	0.1473	5
psi(AcOld+DistMain),p(IsoCorr)	267.81	3.83	0.0275	0.1473	5
psi(forest+DistMain),p(IsoCorr)	267.83	3.85	0.0272	0.1459	5
psi(AcOld+width),p(IsoCorr)	267.98	4	0.0252	0.1353	5

Wild pig					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(.),p(IsoCorr)	208.41	0	0.1202	1	3
psi(width),p(IsoCorr)	208.49	0.08	0.1154	0.9608	4
psi(forest),p(IsoCorr)	208.52	0.11	0.1137	0.9465	4
psi(AcYoung),p(IsoCorr)	208.96	0.55	0.0913	0.7596	4
psi(AcYoung+width),p(IsoCorr)	209.52	1.11	0.069	0.5741	5
psi(DistMain),p(IsoCorr)	209.7	1.29	0.063	0.5247	4
psi(forest+DistMain),p(IsoCorr)	210.12	1.71	0.0511	0.4253	5
psi(AcOld),p(IsoCorr)	210.19	1.78	0.0493	0.4107	4
psi(width+DIstMain),p(IsoCorr)	210.19	1.78	0.0493	0.4107	5
psi(forest+ConnMain),p(IsoCorr)	210.31	1.9	0.0465	0.3867	5
psi(ConnMain),p(IsoCorr)	210.41	2	0.0442	0.3679	4
psi(ConnMain+width),p(IsoCorr)	210.44	2.03	0.0435	0.3624	5
psi(AcOld+width),p(IsoCorr)	210.47	2.06	0.0429	0.357	5
psi(AcYoung+ConnMain),p(IsoCorr)	210.86	2.45	0.0353	0.2938	5
psi(ConnMain+DistMain),p(IsoCorr)	211.68	3.27	0.0234	0.195	5
psi(AcOld+DIstMain),p(IsoCorr)	211.7	3.29	0.0232	0.193	5
psi(AcOld+ConnMain),p(IsoCorr)	212.14	3.73	0.0186	0.1549	5

Mousedeer					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(forest),p(corridor)_GOF	144.94	0	0.1649	1	6
psi(.),p(corridor)	145.38	0.44	0.1323	0.8025	5
psi(width),p(corridor)	146.16	1.22	0.0896	0.5434	6
psi(forest+DistMain),p(corridor)	146.33	1.39	0.0823	0.4991	7

psi(forest+ConnMain),p(corridor)	146.76	1.82	0.0664	0.4025	7
psi(DistMain),p(corridor)	146.81	1.87	0.0647	0.3926	6
psi(ConnMain),p(corridor)	147.15	2.21	0.0546	0.3312	6
psi(AcOld),p(corridor)	147.36	2.42	0.0492	0.2982	6
psi(AcYoung),p(corridor)	147.38	2.44	0.0487	0.2952	6
psi(DistMain+width),p(corridor)	147.83	2.89	0.0389	0.2357	7
psi(ConnMain+width),p(corridor)	147.88	2.94	0.0379	0.2299	7
psi(AcOld+DistMain),p(corridor)	148.09	3.15	0.0341	0.207	7
psi(AcOld+width),p(corridor)	148.11	3.17	0.0338	0.2049	7
psi(AcYoung+width),p(corridor)	148.16	3.22	0.033	0.1999	7
psi(DistMain+ConnMain),p(corridor)	148.49	3.55	0.0279	0.1695	7
psi(AcYoung+ConnMain),p(corridor)	149.02	4.08	0.0214	0.13	7
psi(AcOld+ConnMain),p(corridor)	149.11	4.17	0.0205	0.1243	7

Malay porcupine					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(AcOld+ConnMain),p(setup)_GOF	191.37	0	0.3916	1	5
psi(AcOld),p(setup)	194.74	3.37	0.0726	0.1854	4
psi(AcOld+width),p(setup)	195.29	3.92	0.0552	0.1409	5
psi(forest),p(setup)	195.5	4.13	0.0497	0.1268	4
psi(width),p(setup)	195.67	4.3	0.0456	0.1165	4
psi(.),p(setup)	195.9	4.53	0.0407	0.1038	3
psi(AcYoung+width),p(setup)	196.09	4.72	0.037	0.0944	5
psi(DistMain+ConnMain),p(setup)	196.11	4.74	0.0366	0.0935	5
psi(Forest+DistMain),p(setup)	196.11	4.74	0.0366	0.0935	5
psi(ConnMain),p(setup)	196.22	4.85	0.0346	0.0885	4
psi(DistMain),p(setup)	196.25	4.88	0.0341	0.0872	4
psi(AcYoung),p(setup)	196.39	5.02	0.0318	0.0813	4
psi(ConnMain+width),p(setup)	196.4	5.03	0.0317	0.0809	5
psi(Forest+ConnMain),p(setup)	196.49	5.12	0.0303	0.0773	5
psi(AcOld+DistMain),p(setup)	196.52	5.15	0.0298	0.0762	5
psi(DistMain+width),p(setup)	196.65	5.28	0.0279	0.0714	5
psi(AcYoung+ConnMain),p(setup)	198	6.63	0.0142	0.0363	5

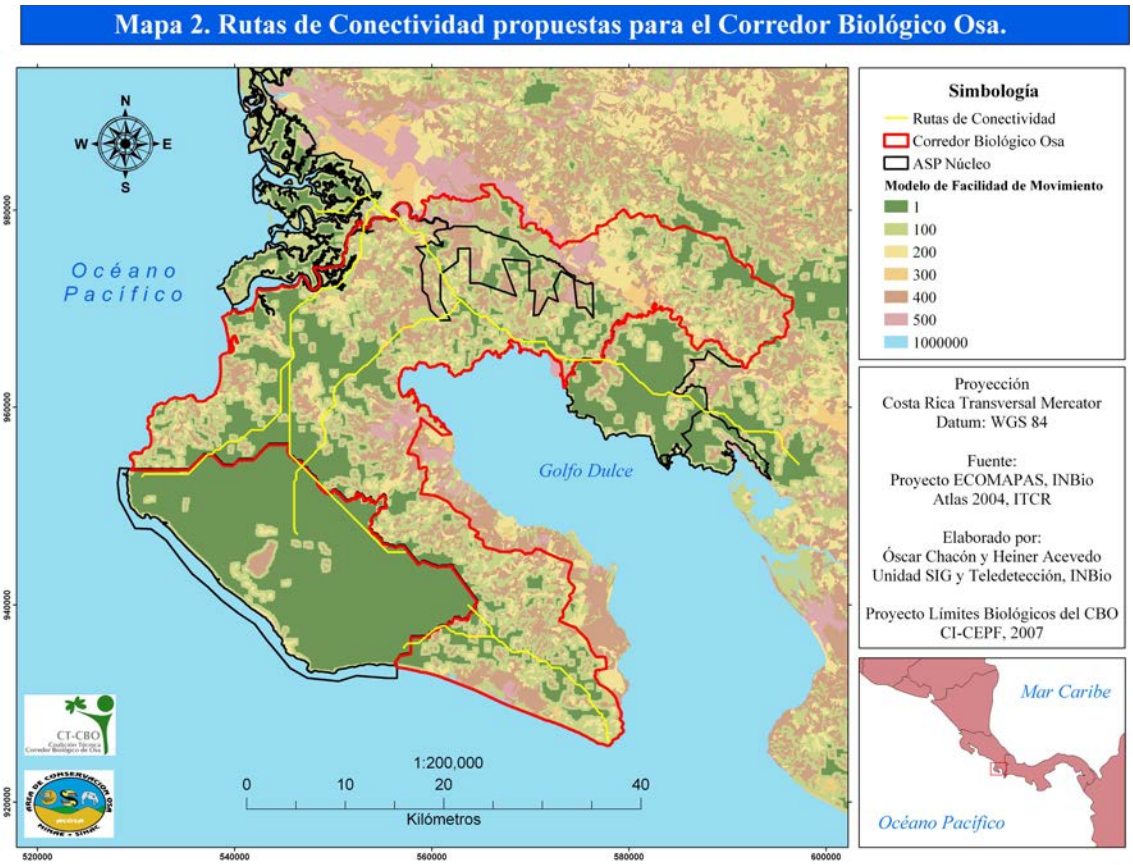
Red muntjac					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(DistMain),p(setup)	217.69	0	0.1832	1	4
psi(DistMain+ConnMain),p(setup)	219.19	1.5	0.0865	0.4724	5
psi(AcYoung),p(setup)	219.61	1.92	0.0701	0.3829	4
psi(DistMain+width),p(setup)	219.65	1.96	0.0688	0.3753	5
psi(AcOld+DistMain),p(setup)	219.67	1.98	0.0681	0.3716	5
psi(forest+DistMain),p(setup)	219.68	1.99	0.0677	0.3697	5
psi(.),p(setup)	219.84	2.15	0.0625	0.3413	3
psi(AcOld),p(setup)	221.1	3.41	0.0333	0.1818	4
psi(ConnMain),p(setup)	221.37	3.68	0.0291	0.1588	4
psi(AcYoung+ConnMain),p(setup)	221.44	3.75	0.0281	0.1534	5

psi(AcYoung+width),p(setup)	221.61	3.92	0.0258	0.1409	5
psi(width),p(setup)	221.83	4.14	0.0231	0.1262	4
psi(forest),p(setup)	221.83	4.14	0.0231	0.1262	4
psi(AcOld+ConnMain),p(setup)	222.88	5.19	0.0137	0.0746	5
psi(AcOld+width),p(setup)	223.1	5.41	0.0122	0.0669	5
psi(ConnMain+width),p(setup)	223.36	5.67	0.0108	0.0587	5
psi(forest+ConnMain),p(setup)	223.37	5.68	0.0107	0.0584	5

Malay civet					
Model	AIC	ΔAIC	AICWt	Model Likelihood	No.Par.
psi(DistMain+width),p(bait)	148.09	0	0.5131	1	5
psi(AcOld+DistMain),p(bait)	149.5	1.41	0.2535	0.4941	5
psi(DistMain),p(bait)	151.21	3.12	0.1078	0.2101	4
psi(forest+DistMain),p(bait)	152.91	4.82	0.0461	0.0898	5
psi(DistMain+ConnMain),p(bait)	152.95	4.86	0.0452	0.088	5
psi(AcOld+width),p(bait)	155.97	7.88	0.01	0.0194	5
psi(AcYoung),p(bait)	156.81	8.72	0.0066	0.0128	4
psi(AcYoung+ConnMain),p(bait)	157.5	9.41	0.0046	0.009	5
psi(.),p(bait)	158.5	10.41	0.0028	0.0055	3
psi(AcYoung+width),p(bait)	158.6	10.51	0.0027	0.0052	5
psi(width),p(bait)	159.17	11.08	0.002	0.0039	4
psi(AcOld),p(bait)	160.07	11.98	0.0013	0.0025	4
psi(ConnMain),p(bait)	160.17	12.08	0.0012	0.0024	4
psi(forest),p(bait)	160.31	12.22	0.0011	0.0022	4
psi(ConnMain+width),p(bait)	160.69	12.6	0.0009	0.0018	5
psi(forest+ConnMain),p(bait)	161.92	13.83	0.0005	0.001	5
psi(AcOld+ConnMain),p(bait)	162.01	13.92	0.0005	0.0009	5

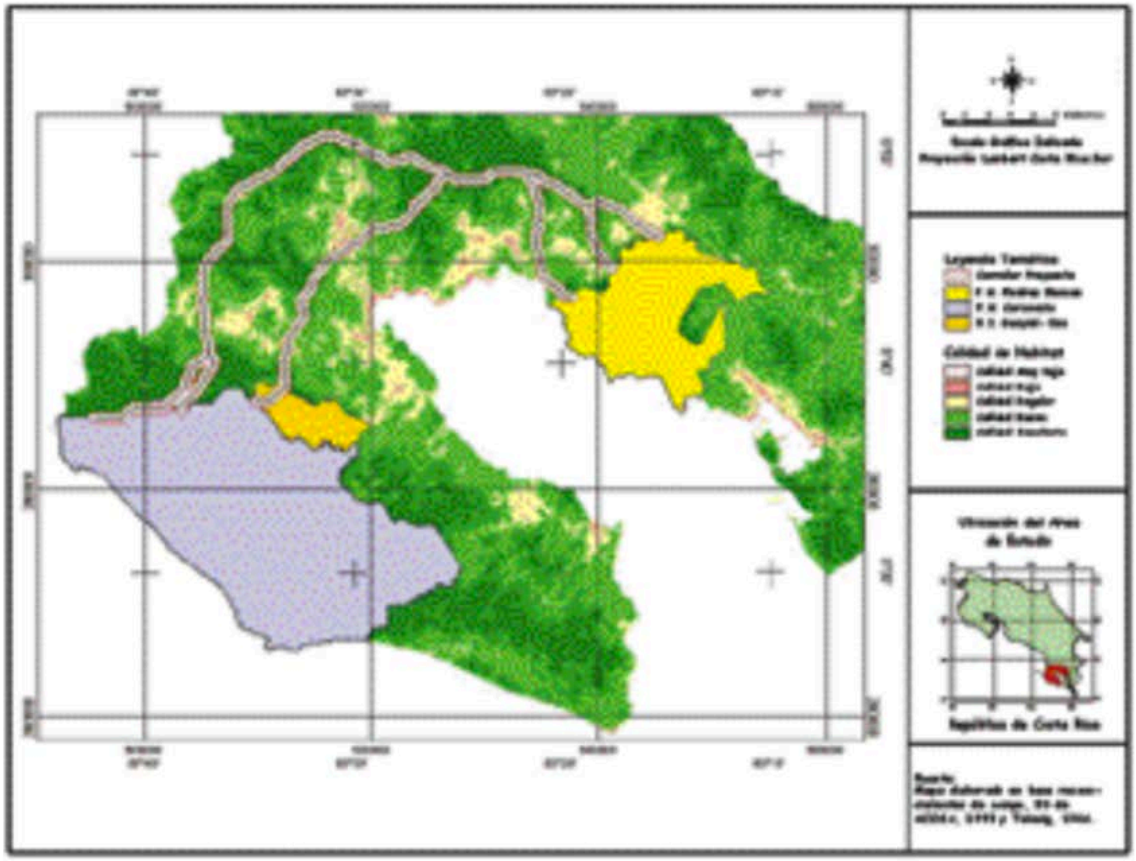
Appendix D. Previous initiatives to model connectivity on the Osa Peninsula

In 2007, the National Biodiversity Institute (INBio) of Costa Rica (as part of a 3-year project implemented by a group of national and international NGOs and government bodies) used least cost path (LCP) modeling to identify the most important passage routes for maintaining connectivity across the peninsula (yellow lines in Map A) based on land cover, slope, and distance to anthropogenic disturbances (Obando and Acevedo 2007). The study did not include biological or empirical data on mammals. The selected routes have not yet been field-tested to confirm that the modeled paths reflect actual use by medium and large mammals.



Map A. Connectivity routes (yellow) and the Osa Biological Corridor (red outline) as proposed by an NGO and government team working to maintain biological connectivity across the Osa Peninsula. Map taken from Obando and Acevedo (2007).

In 2001, Jiménez (2001) modeled connectivity between Corcovado National Park (CNP) and Piedras Blancas National Park (PBNP) for jaguars (Map B). The study used direct and indirect signs to survey felines in primary forest, secondary forest, melina and grasslands and used land cover data and other environmental and anthropogenic variables to model the best connectivity routes for jaguars. The study recommended a minimum of 1 km wide corridors.



Map B. Map of proposed routes, within the Gulfo Dulce Forest Reserve, as possible corridors between Corcovado National Park and Piedras Blancas National Park. Map taken from Jiménez (2001).

Appendix E. Land cover categories for the Costa Rica study area

Land cover categories (Kappelle et al. 2003) from the INOGO Mapas land cover data (Broadbent et al. 2013) that were used in the Costa Rica study. Land cover categories that were dominated by a common feature were merged into combined categories.

INOGO Mapas land cover code	Combined land cover category for this manuscript	Land Use (Spanish)	Frequency in the Osa Peninsula/ Gulfito landscape
1	FOREST	Bosque Denso	Very high
2	FOREST	Bosque Ralo	High
3	GRASSLAND	Herbazal Denso Arbolado	
7	GRASSLAND	Herbazal Denso	High
8	GRASSLAND	Herbazal Ralo	
9	GRASSLAND	Herbazal Arbustivo	
302	GRASSLAND	Herbazal Arbolado para Forraje	
705	GRASSLAND	Herbazal Denso para Forraje	Very High
707	GRASSLAND	Herbazal Denso Quemado	
801	GRASSLAND	Herbazal Ralo para Forraje	Very high
902	GRASSLAND	Herbazal Arbustivo para Forraje	
10	GRASSLAND*	Terreno Descubierto	Very high
702	GRASSLAND*	Herbazal Denso de Arroz	High
101	MANGROVE	Bosque Denso de Mangle	Very high
201	MANGROVE	Bosque Ralo de Mangle	
401	MANGROVE	Matorral Denso de Mangle	
501	MANGROVE	Matorral Ralo de Mangle	
701	MANGROVE	Herbazal Denso de Mangle	
706	MANGROVE*	Herbazal Denso de Negra Forra	
111	OIL PALM	Bosque Denso de Palma de Aceite	Very high
406	OIL PALM	Matorral Denso de Palma de Aceite	
607	OIL PALM	Matorral Denso Arbolado de Palma de Aceite	High
903	OIL PALM	Herbazal Arbustivo de Palma de Aceite	
102	RAPHIA	Bosque Denso de Yolillo	
202	RAPHIA	Bosque Ralo de Yolillo	
301	RAPHIA	Herbazal Arbolado con Yolillo	
402	RAPHIA	Matorral Denso de Yolillo	
901	RAPHIA	Herbazal Arbustivo de Yolillo	
204	RAPHIA*	Bosque Ralo de Cerillo	
604	RAPHIA*	Matorral Denso Arbolado de Cerillo	
4	SHRUBLAND	Matorral Denso	High
5	SHRUBLAND	Matorral Ralo	High
6	SHRUBLAND	Matorral Denso Arbolado	
106	MELINA	Bosque Denso de Melina	
14	WATER BODY	Cuerpo de Agua	High
12	Excluded	Infraestructura	Very high
103	Excluded	Bosque Denso de Trichospermum	
104	Excluded	Bosque Denso de Plantacion Forestal	

INOGO Mapas land cover code	Combined land cover category for this manuscript	Land Use (Spanish)	Frequency in the Osa Peninsula/ Gulfito landscape
105	Excluded	Bosque Denso de Roble Coral	
115	Excluded	Bosque Urbano	
708	Excluded	Herbazal Denso Pantanoso	
90	Excluded	Sombra	
91	Excluded	Nubes	
99	Excluded	Afuera region de estudio INOGO	
100	Excluded	Afuera de imagen RapidEye	
107	Excluded	Bosque Denso de Teca	
108	Excluded	Bosque Denso de Pochote	
109	Excluded	Bosque Denso Pantanoso	
113	Excluded	Bosque Denso de Pejibaye	
203	Excluded	Bosque Ralo de Melina	
205	Excluded	Bosque Ralo de Pejibaye	
304	Excluded	Herbazal Arbolado con Trichospermum	
305	Excluded	Herbazal Arbolado de Negra Forra	
403	Excluded	Matorral Denso de Trichospermum	
404	Excluded	Matorral Denso de Plantacion Forestal	
502	Excluded	Matorral Ralo de Trichospermum	
602	Excluded	Matorral Denso Arbolado de Trichospermum	
603	Excluded	Matorral Denso Arbolado de Plantacion Forestal	
703	Excluded	Herbazal Denso de Banano	
704	Excluded	Herbazal Denso de Bamboo	
802	Excluded	Herbazal Ralo de Negra Forra	

* Land cover categories that were subsequently added to the initial combined categories for occupancy modeling purposes (Chapter 5). The proximity and extent of these land cover categories on the periphery of the study area made these additions necessary.

Appendix F. Occupancy model data from the Costa Rica study site

Table F1. Beta (β) estimates (and 95% credible interval) for multi-species occupancy model. These occupancy values were used to model species distribution (Figure 5.4 in Chapter 5). They include two covariates (Distance to Corcovado NP and Distance to Piedras Blancas NP) that were excluded from connectivity modeling. An asterisks (*) indicates that the credible interval for β did not overlap zero.

	Intercept (Forest)	Distance to Piedras Blancas NP	Distance to Corcovado NP	Shrubland	Grassland	Mangrove	Melina	Oil Palm	*Raphia*	Distance from nearest 500 ha forest block	Distance from river	Road density
AGO	-1.06 ± 0.232 (-1.548--0.651)*	-0.035 ± 0.108 (-0.241-0.181)	-0.256 ± 0.108 (-0.474--0.055)*	0.093 ± 0.043 (0.005-0.175)*	-0.886 ± 0.148 (-1.186--0.611)*	-1.046 ± 0.335 (-1.838--0.514)*	-0.12 ± 0.085 (-0.305-0.021)	-0.662 ± 0.272 (-1.305--0.231)*	-0.282 ± 0.162 (-0.625--0.002)*	-1.434 ± 0.491 (-2.495--0.589)*	-0.187 ± 0.068 (-0.324--0.054)*	-0.072 ± 0.082 (-0.227-0.085)
ARM	-2.133 ± 0.369 (-2.921--1.487)*	-0.061 ± 0.15 (-0.366-0.251)	0.03 ± 0.182 (-0.286-0.402)	0.107 ± 0.054 (0.008-0.226)*	-0.928 ± 0.29 (-1.563--0.424)*	-1.328 ± 0.611 (-2.805--0.429)*	-0.089 ± 0.109 (-0.34-0.086)	0.047 ± 0.202 (-0.37-0.417)	-0.211 ± 0.188 (-0.639-0.095)	-1.186 ± 0.573 (-2.467--0.268)*	-0.073 ± 0.122 (-0.273-0.191)	-0.11 ± 0.124 (-0.351-0.147)
COA	-0.476 ± 0.175 (-0.828--0.134)*	-0.034 ± 0.114 (-0.259-0.201)	-0.215 ± 0.118 (-0.452-0.006)	0.089 ± 0.047 (-0.013-0.177)	-0.449 ± 0.129 (-0.711--0.204)*	-0.883 ± 0.259 (-1.456--0.442)*	0 ± 0.064 (-0.13-0.121)	-0.537 ± 0.241 (-1.106--0.154)*	0.074 ± 0.093 (-0.1-0.262)	-0.318 ± 0.205 (-0.764-0.048)	-0.201 ± 0.081 (-0.373--0.044)*	-0.252 ± 0.112 (-0.491--0.062)*
COY	-3.832 ± 0.664 (-5.148--2.576)*	-0.044 ± 0.198 (-0.442-0.384)	-0.173 ± 0.231 (-0.635-0.321)	0.098 ± 0.061 (-0.026-0.22)	-0.049 ± 0.366 (-0.693-0.705)	-0.871 ± 0.605 (-2.246-0.118)	-0.068 ± 0.152 (-0.432-0.204)	-0.603 ± 0.493 (-1.784-0.15)	-0.184 ± 0.225 (-0.718-0.19)	0.125 ± 0.447 (-0.851-0.909)	-0.177 ± 0.16 (-0.517-0.155)	-0.168 ± 0.175 (-0.553-0.192)
DER	-3.029 ± 0.47 (-3.984--2.16)*	-0.255 ± 0.225 (-0.766-0.076)	-0.092 ± 0.198 (-0.458-0.334)	0.102 ± 0.06 (-0.012-0.233)	-0.822 ± 0.344 (-1.611--0.242)*	-1.087 ± 0.588 (-2.46--0.159)*	0.09 ± 0.119 (-0.119-0.342)	-0.621 ± 0.497 (-1.777-0.101)	-0.238 ± 0.234 (-0.793-0.115)	-0.755 ± 0.63 (-2.161-0.284)	-0.167 ± 0.128 (-0.42-0.107)	-0.274 ± 0.189 (-0.74-0.004)
JAG	-3.954 ± 0.539 (-5.12--2.982)*	-0.158 ± 0.206 (-0.649-0.179)	0.064 ± 0.265 (-0.342-0.672)	0.097 ± 0.061 (-0.026-0.222)	-0.424 ± 0.337 (-1.103-0.233)	-0.904 ± 0.593 (-2.291-0.043)	-0.087 ± 0.151 (-0.464-0.149)	-0.551 ± 0.484 (-1.648-0.226)	-0.169 ± 0.217 (-0.665-0.209)	-0.696 ± 0.653 (-2.169-0.396)	-0.12 ± 0.154 (-0.396-0.25)	-0.244 ± 0.195 (-0.722-0.062)
JGI	-3.208 ± 0.504 (-4.217--2.241)*	-0.088 ± 0.192 (-0.526-0.279)	-0.071 ± 0.22 (-0.473-0.422)	0.09 ± 0.061 (-0.043-0.202)	-0.43 ± 0.31 (-1.051-0.171)	-1.033 ± 0.583 (-2.364--0.116)*	-0.087 ± 0.149 (-0.438-0.155)	-0.672 ± 0.483 (-1.83-0.029)	-0.076 ± 0.177 (-0.444-0.286)	0.295 ± 0.358 (-0.47-0.935)	-0.192 ± 0.153 (-0.528-0.107)	-0.26 ± 0.199 (-0.758-0.041)
MAR	-2.285 ± 0.425 (-3.112--1.428)*	-0.102 ± 0.17 (-0.471-0.211)	-0.111 ± 0.189 (-0.467-0.287)	0.101 ± 0.058 (-0.012-0.226)	-0.696 ± 0.305 (-1.358--0.159)*	-0.63 ± 0.386 (-1.481-0.032)	-0.118 ± 0.156 (-0.503-0.107)	-0.7 ± 0.492 (-1.852-0.01)	-0.27 ± 0.23 (-0.81-0.061)	-0.085 ± 0.375 (-0.898-0.57)	-0.103 ± 0.14 (-0.34-0.218)	-0.192 ± 0.155 (-0.547-0.087)
OCE	-1.45 ± 0.228 (-1.916--1.011)*	0.082 ± 0.173 (-0.198-0.476)	-0.196 ± 0.158 (-0.515-0.122)	0.087 ± 0.057 (-0.045-0.186)	-0.331 ± 0.189 (-0.707-0.03)	-0.592 ± 0.314 (-1.298--0.082)*	-0.092 ± 0.121 (-0.371-0.099)	-0.29 ± 0.214 (-0.76-0.088)	-0.152 ± 0.135 (-0.444-0.086)	0.001 ± 0.211 (-0.458-0.378)	-0.153 ± 0.115 (-0.382-0.084)	-0.131 ± 0.123 (-0.377-0.128)
PAC	-1.995 ± 0.302 (-2.637-	-0.083 ± 0.139 (-0.375-	-0.238 ± 0.143 (-0.539-	0.096 ± 0.052 (-0.012-	-0.72 ± 0.216 (-1.18--0.34)*	-0.704 ± 0.314 (-1.409-	-0.045 ± 0.095 (-0.257-	-0.768 ± 0.501 (-2.022-	-0.159 ± 0.164 (-0.513-	-1.257 ± 0.574 (-2.484-	-0.208 ± 0.102 (-0.429-	-0.207 ± 0.126 (-0.495-

	Intercept (Forest)	Distance to Piedras Blancas NP	Distance to Corcovado NP	Shrubland	Grassland	Mangrove	Melina	Oil Palm	*Raphia*	Distance from nearest 500 ha forest block	Distance from river	Road density
	-1.456)*	0.18)	0.033)	0.201)		-0.172)*	0.129)	-0.101)*	0.129)	-0.296)*	-0.013)*	0.012)
PEC	-1.514 ± 0.252 (-2.043--1.055)*	0.111 ± 0.184 (-0.18-0.52)	-0.486 ± 0.198 (-0.874--0.127)*	0.097 ± 0.05 (-0.007-0.197)	-0.708 ± 0.19 (-1.105--0.356)*	-1.277 ± 0.462 (-2.38--0.558)*	-0.081 ± 0.108 (-0.332-0.097)	-0.689 ± 0.335 (-1.479--0.191)*	-0.061 ± 0.11 (-0.281-0.161)	-0.291 ± 0.286 (-0.904-0.221)	-0.225 ± 0.102 (-0.451--0.043)*	-0.294 ± 0.151 (-0.646--0.06)*
PUM	-3.056 ± 0.53 (-4.136--2.033)*	-0.174 ± 0.199 (-0.649-0.143)	-0.028 ± 0.217 (-0.395-0.439)	0.091 ± 0.06 (-0.041-0.203)	-0.58 ± 0.328 (-1.263-0.031)	-0.423 ± 0.406 (-1.304-0.286)	-0.102 ± 0.154 (-0.476-0.134)	-0.588 ± 0.495 (-1.789-0.153)	-0.203 ± 0.231 (-0.742-0.17)	-1.027 ± 0.722 (-2.702-0.137)	-0.113 ± 0.145 (-0.36-0.223)	-0.285 ± 0.213 (-0.839-0.017)
RAC	-0.758 ± 0.145 (-1.047--0.48)*	-0.093 ± 0.115 (-0.327-0.124)	-0.147 ± 0.106 (-0.35-0.071)	0.1 ± 0.049 (0.002-0.199)*	-0.011 ± 0.138 (-0.282-0.255)	0.507 ± 0.085 (0.338-0.67)*	0.09 ± 0.089 (-0.072-0.265)	-0.003 ± 0.122 (-0.251-0.227)	0.013 ± 0.1 (-0.175-0.216)	0.385 ± 0.084 (0.221-0.543)*	-0.368 ± 0.177 (-0.777--0.118)*	-0.066 ± 0.109 (-0.262-0.164)
SKU	-2.343 ± 0.38 (-3.128--1.632)*	-0.1 ± 0.162 (-0.456-0.208)	-0.087 ± 0.182 (-0.422-0.296)	0.092 ± 0.058 (-0.031-0.2)	-0.641 ± 0.271 (-1.223--0.161)*	-1.217 ± 0.603 (-2.608--0.298)*	-0.028 ± 0.111 (-0.27-0.177)	-0.702 ± 0.495 (-1.935--0.015)*	-0.062 ± 0.155 (-0.375-0.252)	-0.313 ± 0.408 (-1.203-0.387)	-0.11 ± 0.132 (-0.334-0.184)	-0.163 ± 0.142 (-0.47-0.113)
TAP	-3.911 ± 0.653 (-5.213--2.663)*	-0.159 ± 0.213 (-0.676-0.184)	-0.068 ± 0.234 (-0.483-0.455)	0.108 ± 0.064 (-0.005-0.255)	-0.606 ± 0.366 (-1.412-0.053)	-0.868 ± 0.598 (-2.191-0.133)	-0.079 ± 0.153 (-0.439-0.17)	-0.548 ± 0.489 (-1.711-0.243)	-0.178 ± 0.225 (-0.707-0.197)	-0.692 ± 0.686 (-2.267-0.439)	-0.178 ± 0.155 (-0.507-0.148)	-0.234 ± 0.195 (-0.712-0.08)
TAY	-2.249 ± 0.378 (-3.039--1.558)*	-0.048 ± 0.149 (-0.343-0.266)	-0.134 ± 0.158 (-0.439-0.19)	0.097 ± 0.055 (-0.015-0.208)	-0.766 ± 0.281 (-1.367--0.265)*	-0.519 ± 0.33 (-1.25-0.044)	-0.083 ± 0.12 (-0.367-0.108)	-0.691 ± 0.491 (-1.884--0.013)*	-0.163 ± 0.183 (-0.57-0.15)	-1.298 ± 0.664 (-2.789--0.204)*	-0.125 ± 0.12 (-0.349-0.142)	-0.163 ± 0.13 (-0.444-0.086)

AGO = Agouti, ARM = Armadillo, COA = Coati, COY = Coyote, DER = Red brocket deer, JAG = Jaguar, JGI = Jaguarundi, MAR = Margay, OCE = Ocelot, PAC = Paca, PEC = Collared peccary, PUM = Puma, RAC = Raccoon, SKU = Striped hog-nosed skunk, TAP = Tapir, TAY = Tayra. For further information on each species refer to Table 5.3 in Chapter 5.

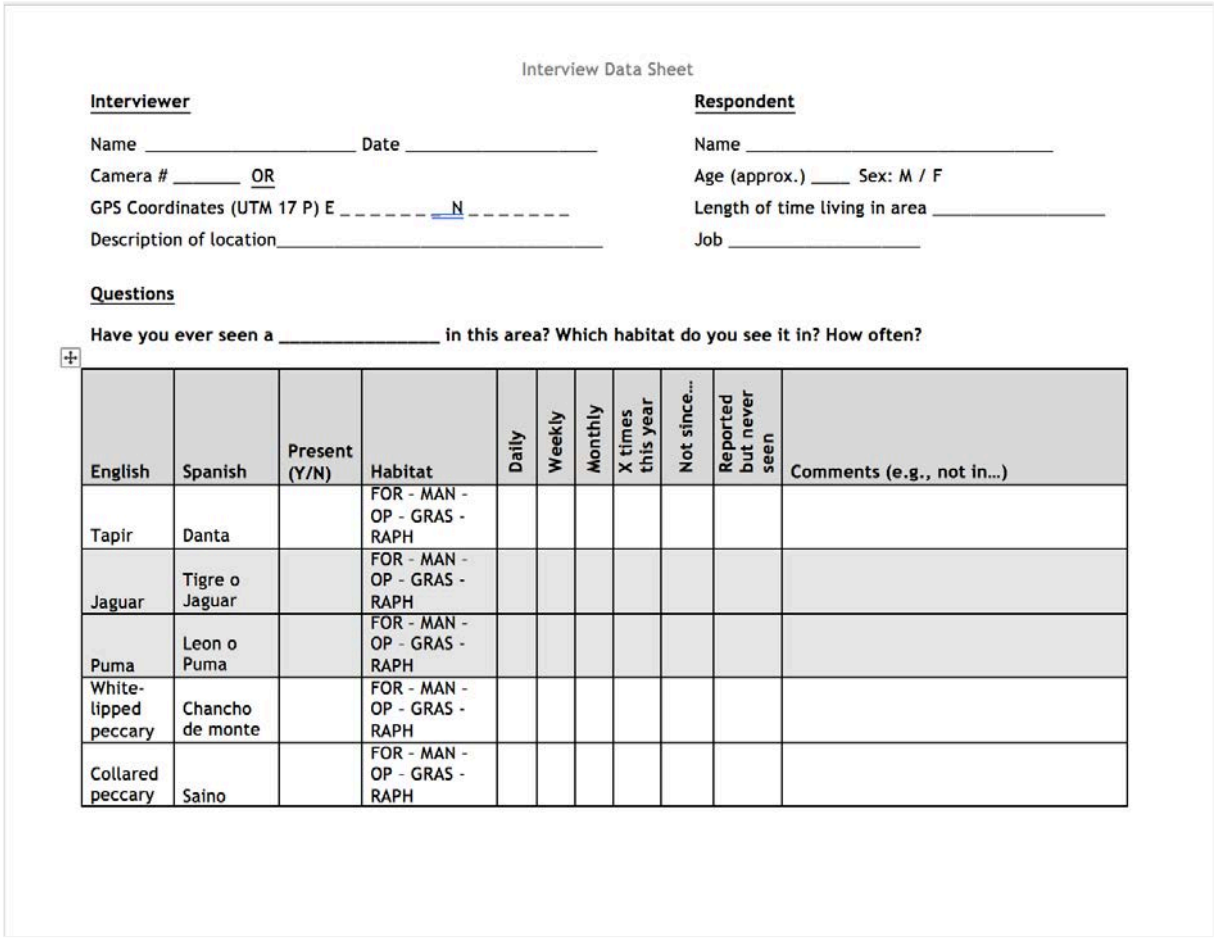
Table F2. Beta (β) estimates (and 95% credible interval) for detection probability in multi-species occupancy models used for modeling species distribution. An asterisks (*) indicates that the credible interval for β did not overlap zero.

	SeasonDry (Intercept)	SeasonTransition	SeasonWet
AGO	-2.311 ± 0.124 (-2.554--2.072)*	-0.057 ± 0.158 (-0.372-0.261)	0.607 ± 0.146 (0.325-0.896)*
ARM	-3.452 ± 0.296 (-4.069--2.914)*	-0.003 ± 0.24 (-0.47-0.535)	0.593 ± 0.291 (0.039-1.185)*
COA	-3.113 ± 0.16 (-3.428--2.803)*	-0.234 ± 0.215 (-0.708-0.117)	0.48 ± 0.18 (0.131-0.833)*
COY	-3.674 ± 0.534 (-4.834--2.735)*	-0.055 ± 0.307 (-0.724-0.584)	-0.184 ± 0.687 (-1.676-1.049)
DER	-3.161 ± 0.307 (-3.805--2.607)*	0.083 ± 0.263 (-0.348-0.697)	-0.699 ± 0.636 (-2.054-0.385)
JAG	-3.251 ± 0.428 (-4.134--2.459)*	-0.068 ± 0.283 (-0.678-0.506)	0.901 ± 0.513 (0.009-1.995)*
JGI	-3.588 ± 0.434 (-4.53--2.816)*	-0.086 ± 0.322 (-0.794-0.538)	-0.259 ± 0.511 (-1.366-0.617)
MAR	-3.917 ± 0.439 (-4.853--3.147)*	0.072 ± 0.28 (-0.396-0.733)	0.043 ± 0.409 (-0.82-0.816)
OCE	-3.387 ± 0.259 (-3.92--2.908)*	0.11 ± 0.269 (-0.311-0.744)	0.598 ± 0.288 (0.07-1.189)*
PAC	-2.749 ± 0.193 (-3.149--2.391)*	0.052 ± 0.216 (-0.322-0.538)	0.084 ± 0.239 (-0.378-0.556)
PEC	-2.85 ± 0.189 (-3.231--2.494)*	0.02 ± 0.195 (-0.337-0.448)	-0.292 ± 0.239 (-0.76-0.185)
PUM	-3.827 ± 0.48 (-4.877--2.984)*	0.087 ± 0.295 (-0.381-0.817)	-0.049 ± 0.458 (-1.033-0.804)
RAC	-2.719 ± 0.159 (-3.03--2.414)*	-0.148 ± 0.183 (-0.538-0.178)	0.269 ± 0.189 (-0.107-0.646)
SKU	-3.562 ± 0.344 (-4.285--2.936)*	0.079 ± 0.266 (-0.358-0.716)	0.053 ± 0.359 (-0.648-0.74)
TAP	-3.599 ± 0.517 (-4.724--2.711)*	0.014 ± 0.283 (-0.5-0.683)	-0.244 ± 0.699 (-1.806-1.017)
TAY	-3.387 ± 0.266 (-3.942--2.884)*	-0.075 ± 0.229 (-0.569-0.39)	0.082 ± 0.33 (-0.579-0.721)

AGO = Agouti, ARM = Armadillo, COA = Coati, COY = Coyote, DER = Red brocket deer, JAG = Jaguar, JGI = Jaguarundi, MAR = Margay, OCE = Ocelot, PAC = Paca, PEC = Collared peccary, PUM = Puma, RAC = Raccoon, SKU = Striped hog-nosed skunk, TAP = Tapir, TAY = Tayra. For further information on each species refer to Table 5.3 in Chapter 5.

Appendix G. Interview data sheet for community interviews in Costa Rica

Front page of data sheet filled out by interviewer while interviewing community members as described in Chapter 7.



Interview Data Sheet

Interviewer

Name _____ Date _____

Camera # _____ OR

GPS Coordinates (UTM 17 P) E _ _ _ _ _ _ N _ _ _ _ _ _ _

Description of location_____

Respondent

Name _____

Age (approx.) ____ Sex: M / F

Length of time living in area _____

Job _____

Questions

Have you ever seen a _____ in this area? Which habitat do you see it in? How often?

English	Spanish	Present (Y/N)	Habitat	Daily	Weekly	Monthly	X times this year	Not since...	Reported but never seen	Comments (e.g., not in...)
Tapir	Danta		FOR - MAN - OP - GRAS - RAPH							
Jaguar	Tigre o Jaguar		FOR - MAN - OP - GRAS - RAPH							
Puma	Leon o Puma		FOR - MAN - OP - GRAS - RAPH							
White-lipped peccary	Chancho de monte		FOR - MAN - OP - GRAS - RAPH							
Collared peccary	Saino		FOR - MAN - OP - GRAS - RAPH							

Back page of data sheet filled out by interviewer while interviewing community members as described in Chapter 7.

Interview Data Sheet

English	Spanish	Present (Y/N)	Habitat	Daily	Weekly	Monthly	X times this year	Not since...	Reported but never seen	Comments (e.g., not in...)
Coyote	Coyote		FOR - MAN - OP - GRAS - RAPH							
Spider Monkey	Araña, colorado		FOR - MAN - OP - GRAS - RAPH							
Squirrel Monkey	Titi, ardilla		FOR - MAN - OP - GRAS - RAPH							
Howler Monkey	Congo, aullador		FOR - MAN - OP - GRAS - RAPH							
Capuchin	Mono carablanca		FOR - MAN - OP - GRAS - RAPH							
Red-brocket deer	Cabro de monte		FOR - MAN - OP - GRAS - RAPH							
White tailed deer	Venado colablanca		FOR - MAN - OP - GRAS - RAPH							

Hunting

Which species are hunted in your area?

Do you think the population of any of these species has changed as a result of hunting?